



The dinoflagellate cyst genera *Achomosphaera* Evitt 1963 and *Spiniferites* Mantell 1850 in Pliocene to modern sediments

a summary of round table discussions

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The dinoflagellate cyst genera *Achomosphaera* Evitt 1963 and *Spiniferites* Mantell 1850 in Pliocene to modern sediments: a summary of round table discussions

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ABSTRACT

We present a summary of two round-table discussions held during two subsequent workshops in Montreal (Canada) on 16 April 2014 and Ostend (Belgium) on 8 July 2015. Five species of the genus *Achomosphaera* Evitt 1963 and 33 of the genus *Spiniferites* Mantell 1850 emend. Sarjeant 1970 occurring in Pliocene to modern sediments are listed and briefly described along with remarks made by workshop participants. In addition, several holotypes and topotypes are reillustrated. Three species previously assigned to *Spiniferites* are here considered/accepted as belonging to other genera: *Impagidinium inaequalis* (Wall and Dale in Wall et al. 1973) Londeix et al. 2009, *Spiniferites? rubinus* (Rossignol 1962 ex Rossignol 1964) Sarjeant 1970, and *Thalassiphora balcanica* Baltes, 1971. This summary forms the basis for a set of papers that follows, where points raised during the workshops are explored in greater detail.

KEYWORDS

Spiniferites; *Achomosphaera*;
Hafniasphaera;
Rottnestia; *Pterocysta*

1. Introduction

This chapter summarises discussions on the dinoflagellate cyst genera *Achomosphaera* Evitt 1963 and *Spiniferites* Mantell 1850 emend. Sarjeant 1970 held during two workshops. The first took place at GEOTOP, Université du Québec à Montréal (UQAM), in Montreal (Canada) on 16

April 2014. During this workshop, all *Spiniferites* and *Achomosphaera* species recorded in Quaternary deposits were discussed individually by the participants. Several issues were noted regarding their classification/description, and suggestions were made as how to resolve such issues. Several of the problems were further considered during a follow-up workshop at the Flanders Marine

Institute (VLIZ) in Ostend (Belgium), where a round-table discussion was held on 8 July 2015. Notes made by NV and PG during the discussions were summarised afterwards by NV, PG and KNM and form the basis of this document.

The aim of the workshops was to evaluate the taxonomy and nomenclature of those taxa assigned to the genera *Achomosphaera* and *Spiniferites* that have been recorded in Pliocene to modern sediment. We have compiled all relevant information on these taxa and reillustrated selected holotypes and topotypes. A generic overview that includes other related genera can be found in Mertens & Carbonell-Moor (2018). We have excluded some Paratethyan taxa (i.e., species described from deposits of the Paratethys Sea, notably in the Pannonian, Vienna, Molasse and Ponto-Caspian basins) that, according to PJM, lack unambiguous age constraints for a Pliocene to modern occurrence (e.g., *Spiniferites maisensis* Sütő 1994 and *Spiniferites virgulaeformis* Sütő 1994). All taxa belonging to *Achomosphaera* or *Spiniferites* that are currently known from Pliocene to modern sediments are listed alphabetically in Section 2. Species previously assigned to *Spiniferites* or *Achomosphaera*, but now considered to belong to other genera, are listed alphabetically in Section 3. Note that the views presented here reflect a broad consensus, and do not necessarily imply full agreement among the panelists. Authorships for all taxonomic names cited are provided in Supplementary Appendix 1 and 2. We have updated stratigraphic ranges where possible to allow for the lowering of the base of the Pleistocene in 2009 from the base of the Calabrian Stage to that of the Gelasian Stage, effectively from 1.8 to 2.6 Ma. A consequence was the readjustment of the Piacenzian from Middle Pliocene, which had become irrelevant, to Upper Pliocene (Gibbard and Head 2010; Head and Gibbard 2015).

2. Discussion of taxa belonging to the genera *Achomosphaera* and *Spiniferites* occurring in Pliocene to modern sediments

II taxa are listed alphabetically with their synonyms (with related comments in brackets) and other relevant information. Distinguishing characters are described using existing literature that has been paraphrased and updated with modern terminology. Intraspecific morphotypes here refer to formal subspecies (or varieties) that have been described, or informal morphologies described in the literature. Points from the discussions that arose during the workshops are documented in the remarks section for each species described, and elsewhere where appropriate. Often, no agreement could be reached to make any formal changes, and this document then reflects this disagreement. For example, some participants preferred to use *Spiniferites multispheeratus*, while others considered this species to belong to *Hafniasphaera*; such disagreements are left open in this summary. For wall structure, we follow terminology used by Head (1994). Measurements are those given in cited references. Kofoidian nomenclature is used to designate the

plate numbers. For simplicity, we choose not to use 'para-' terminology to distinguish features of cysts from their motile counterparts, since only cyst morphology is addressed here.

2.1. *Achomosphaera andalousiensis* Jan du Chêne 1977 emend. Jan du Chêne and Londeix 1988

Synonymy. "*Achomosphaera perforata*"; Morzadec-Kerfourn 1979, pl. 31, figs. 1–2, 4; 1984, pl. II, figs. 13–14.

non *Spiniferites septentrionalis* Harland 1979, p. 103–104, pl. 1, figs. 12–18; text-fig. 4.

Holotype. Jan du Chêne 1977, pl. 1, fig. 1, lost according to Jan du Chêne & Londeix (1988, p. 237).

Lectotype. Jan du Chêne and Londeix (1988, p. 244, pl. 1, fig. 1–3).

Type locality. Carmona section, Andalusia, Spain.

Type stratum. Upper Miocene (Jan du Chêne 1977).

Etymology. Derived from the type locality (Jan du Chêne 1977).

Distinguishing characters. Ellipsoid central body bearing long, slender processes. The pedium is thin and smooth, the tegillum is thick and smooth to shagreenate. Pedium and tegillum are closely appressed, except below the processes, which are formed by the tegillum. The processes are gonol and long, slender, hollow, and sometimes fenestrate at their bases, and terminate distally in characteristic fenestrate platforms. Some adjacent processes (often in apical or circular areas) are connected by crests. The sulcus is indicated by small processes with bifid distal ends; sutural ornamentation is completely absent. The archeopyle is formed by loss of plate 3'', the operculum is free. (Based on Jan du Chêne 1977, p. 112, and Jan du Chêne & Londeix 1988, p. 239–241.)

Dimensions. Central body length 40–50 µm, width 34–44 µm; process length 14–26 µm, width of distal ends 14–21 µm (Jan du Chêne & Londeix 1988).

Biological affinity. Unknown.

Intraspecific morphotypes. *Achomosphaera andalousiensis* subsp. *suttonensis* Head 1997 has many fenestrations in the distal platforms of the processes and was described from the Lower Pliocene of eastern England (Head 1997). *Achomosphaera andalousiensis* subsp. *andalousiensis* (autonym) has notably fewer fenestrations in the distal platforms of the processes.

Comparison. For *Spiniferites septentrionalis*, see Section 2.35. *Spiniferites speetonensis* from the Lower Cretaceous has similar distal process endings but differs in having intergonal processes and sutures (Jan du Chêne & Londeix 1988). *Spiniferites perforatus* from the Lower Eocene differs from *Achomosphaera andalousiensis* in having intergonal processes and sutures that are sometimes elevated (Jan du Chêne & Londeix 1988).

Remarks. *Spiniferites septentrionalis* is a junior synonym according to Harland (1983, p. 103–104), whose opinion was followed by Jan du Chêne & Londeix (1988, p. 421) but questioned by Head & Wrenn (1992, p. 2) and not accepted here.

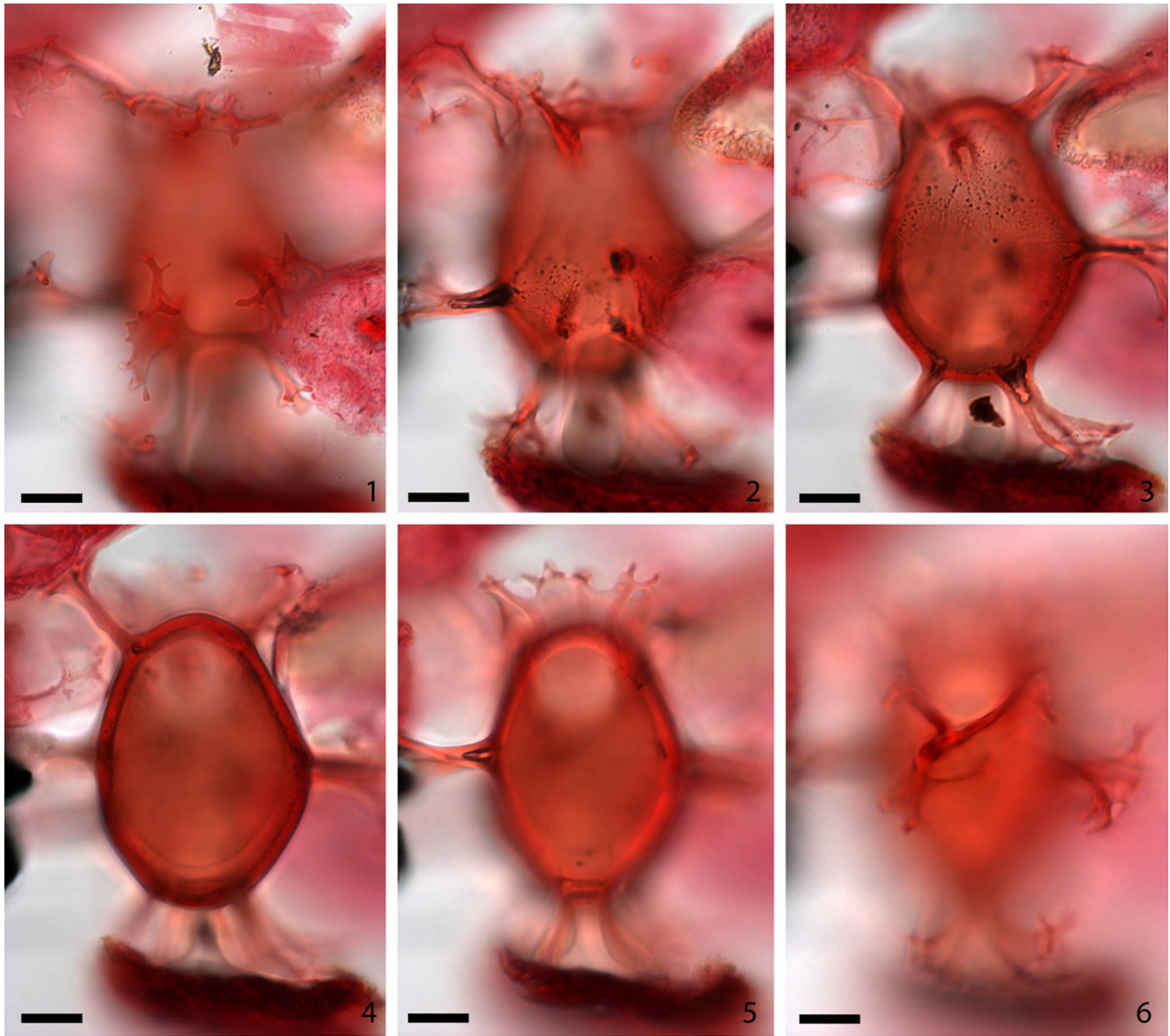


Plate 1. 1–6. *Achomosphaera argesensis* Demetrescu 1989 from S4677 Hungary FI-2007-001 at high to low focus; note hollow bases of processes (shown by bubbles present in 2–3), visible tabulation (3), thick wall (4) and high crest above archeopyle (5). Slide provided by VTT, photographed by KNM. All scale bars = 10 μ m.

“Achomosphaera perforata” of Morzadec-Kerfourn 1979 from the Lower Holocene of Tunisia, as remarked by LL and KNM, it is unclear whether Morzadec-Kerfourn (1979) incorrectly used this name to refer to *Achomosphaera ramulifera* var. *perforata* from the Lower Eocene (later transferred to *Achomosphaera ramulifera* subsp. *perforata*) or intended to propose a new combination. Either way, Morzadec-Kerfourn did not validly publish the name *Achomosphaera perforata*. Morzadec-Kerfourn (1979) synonymised *Achomosphaera andalousiensis* and *“Achomosphaera septentrionalis”* with *Achomosphaera ramulifera* subsp. *perforata*; we do not agree with this synonymy.

There is some doubt about the stratigraphic range of *Achomosphaera andalousiensis* (see e.g., Head 1996a, p. 1207), but if the specimens of Morzadec-Kerfourn (1979) from the Upper Pleistocene to Upper Holocene of Tunisia are *in situ*, the species ranges from the Serravallian

(Middle Miocene; Dybkjaer & Piasecki 2010) to the Late Holocene.

2.2. *Achomosphaera argesensis* Demetrescu 1989 (Plate 1, figures 1–6)

Synonymy. None.

Holotype. Demetrescu 1989, pl. 1, figs. 1–5; text-fig. 2; text-fig. 3A, C.

Type locality. No specific type locality was clearly specified by Demetrescu (1989), but it is presumably somewhere in the Argeş region of Romania.

Type stratum. Lower Pliocene of the southern Carpathians foredeep (Demetrescu 1989).

Etymology. Named after the Argeş region of Romania (Demetrescu 1989).

Distinguishing characters. Ovoid central body with a pronounced apical boss and lacking sutural ornamentation. The outer surface is smooth, and bears 24 lobate, branched, exclusively gonol processes, which can have fenestrate bases. The processes are hollow or sometimes partly solid. Their distal ends expand into lobate short branches, and some have irregularly fringed tips. Two of the apical processes are fused and have a flattened distal end, which can also be the case for two of the antapical processes. Expressed tabulation is 4', 6'', 6c, 7s, 5-76''', 1p, 1'''''. The ends of the cingulum are displaced by apparently about one cingulum width, and the sulcus is straight. The archeopyle is formed by loss of plate 3'' and the operculum is free. (Based on Demetrescu 1989, p. 51–53.)

Dimensions. Central body length 47–50 µm, width 32–35 µm, thickness 33–35 µm; apical boss 1–7 µm long; process length 15–26 µm (Demetrescu 1989).

Biological affinity. Unknown.

Intraspecific morphotypes. None.

Comparison. *Achomosphaera argensis* differs from *Achomosphaera ramulifera* in having an apical boss which resembles that of *Achomosphaera improcera* Islam 1983 from the Eocene and *Spiniferites bentorii*, but *Achomosphaera improcera* has much shorter processes, and *Spiniferites bentorii* has low sutures. *Achomosphaera argensis* also resembles *Achomosphaera andalousiensis*, but the latter does not have a flat apical process or processes with lobate tips. *Spiniferites validus* Sütő-Szentai 1982, described from the Pannonian Basin, differs from *Achomosphaera argensis* in having a thin, elongated apical process instead of a large flattened apical process. (Based on Demetrescu 1989.)

Remarks. PJM was unsuccessful in locating the holotype in Bucharest because the Institute of Geology Bucharest has been dismantled and the location of the type slides is no longer known; moreover, it was not possible to contact Emanuel Demetrescu, so the holotype is effectively lost. Eaton (1996, pl. IV, figs. 6–7) illustrated well-preserved specimens from the Black Sea with membranes connecting the distal ends of apical and antapical gonol processes; Eaton's slides are archived in the Palynological Slide Collection of the Department of Paleontology at the Natural History Museum, London, U.K. The age of Eaton's sample is uncertain. VT noted that he saw specimens of *Achomosphaera argensis* from the Pannonian Basin. However, based on the original publication of Demetrescu (1989), VT identified *Achomosphaera argensis* on the basis that the holotype illustrations show clear membranes connecting the gonol processes associated with the apical plates. He suggested that this is the criterion to consider in separating *Achomosphaera argensis* from the other species described from the Pannonian Basin/Paratethys. AG agreed that it is very distinct and suggested that these forms of *Achomosphaera* may fit better in *Spiniferites*. During the drafting of this report, LL remarked that a lack of true septa between most processes would still leave *Achomosphaera argensis* in *Achomosphaera*. FS noted during drafting that she observed *Achomosphaera argensis* in Upper Miocene (regional Pontian Stage) sediments of the Paratethyan Black Sea.

2.3. *Achomosphaera callosa* Matsuoka 1983 (Plate 2, figures 1–3)

Synonymy. None.

Holotype. Matsuoka 1983, pl. 11, figs. 6a–c.

Type locality. Ota, Tsugawa-cho, Niigata Prefecture, central Japan.

Type stratum. Tokonami Formation, equivalent to the Nishiyama Formation; Pliocene (Matsuoka 1983).

Etymology. From Latin, *callosa*, thick skinned, in reference to the thick wall (Matsuoka 1983).

Distinguishing characters. Central body thick-walled, spheroidal to (rarely) ovoid with a coarsely granular outer surface. The smooth processes are gonol only, and sutural septa are only occasionally present. The archeopyle is formed by loss of plate 3'' and is reduced. (Based on Matsuoka 1983, p. 128–129.)

Dimensions. Central body length 36–53 µm, width 36–45 µm, wall thickness up to 3 µm; process length up to 15 µm (Matsuoka 1983, p. 128).

Biological affinity. Unknown.

Intraspecific morphotypes. None.

Comparison. *Achomosphaera callosa* resembles *Achomosphaera crassipellis* (Deflandre & Cookson 1955) Stover & Evitt 1978, and *Achomosphaera* cf. *sagena* Davey & Williams 1966 of Gocht (1969, p. 36, pl. 7, figs. 1–2), but differs from these two forms in having a coarsely granular outer surface and exclusively gonol processes (Matsuoka 1983). The central body of *Achomosphaera crassipellis* is larger (74–89 µm) than that of *Achomosphaera callosa*, and has a thicker wall judging from the illustration in Deflandre & Cookson (1955, no measurements provided) and longer processes (23–26 µm) (measurements from Deflandre & Cookson 1955).

Remarks. Matsuoka (1983, p. 128–129) described *Achomosphaera callosa* from the Pliocene and Lower Pleistocene of Japan. LL expressed that he has no problem with the species, although he has not observed it in Quaternary sediments. The exact range of the species remains to be determined. MJH remarked that the central body apparently has a solid pedium, a prismatic layer on top and open luxuria, but no tegillum. This leads to the question of what the processes are made of, an issue probably best answered through scanning electron microscopy. Other than that, MJH considers *Achomosphaera callosa* a distinctive species, and LL agrees.

2.4. *Achomosphaera granulata* Mao Shaozhi 1989

Synonymy. Non *Achomosphaera* sp. A of Matsuoka 1983, pl. 11, figs. 1–5, illustrated in Plate 2, figures 4–8.

Holotype. Mao Shaozhi 1989, pl. 28, fig. 10.

Type locality. Northern Xisha Trench, South China Sea.

Type stratum. Upper Pleistocene (Mao Shaozhi 1989).

Etymology. Derived from the occurrence of dense granules on the wall and processes (Mao Shaozhi 1989).

Distinguishing characters. Central body ovoid, thick-walled, light brown to brown, commonly with a short apical boss.

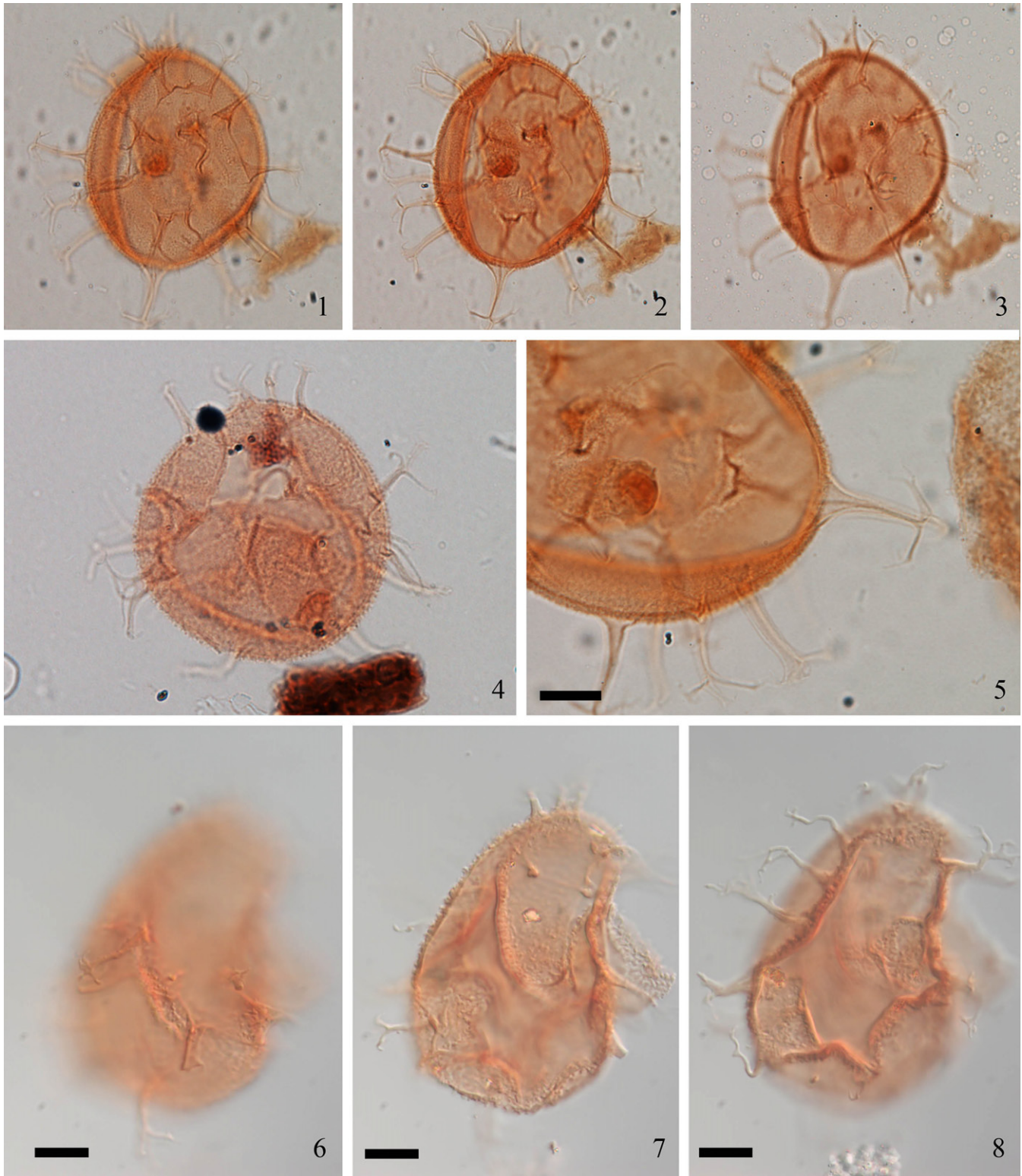


Plate 2. 1–3. Holotype of *Achromosphaera callosa* Matsuoka 1983 at high to low focus. 4. Topotype. 5. Focus on holotype showing detail of wall texture and process. 6–8. Upper to lower focus of *Achromosphaera* sp. A of Matsuoka (1983), plate 11, figures 1–5 [Mao Shaozhi (1989) considered her specimens of *Achromosphaera granulata* the same as these specimens from the Lower to Upper Miocene of the Niigata district (central Japan), but we disagree with this assessment]. Slides provided by KM, photographed by KNM. All scale bars = 10 μ m.

The apical horn has a basal width greater than its length (typically 3–5 μ m) and has a truncated distal end. The cingulum is 5–7 μ m wide, delimited by dense granules, separating the cyst into a sub-triangular epicyst and rounded to nearly trapezoidal hypocyst. There are two wall layers, the thick

outer wall forming the exclusively gonal processes. The surface of the outer wall is ornamented by dense and well-distributed granules. The granules are coarse and sometimes link to form curved lines. They are developed on both the central body and processes, and make the outline of the

processes rough. The processes can be perforated due to corrosion according to Mao Shaozhi (1989). The processes have wide bases and taper rapidly. No sutures are present except for the granules that mark the cingulum dorsally. The archeopyle is formed by loss of plate 3". (Based on Mao Shaozhi 1989, p. 139, translated from Chinese by HG, and observations of *Achomosphaera* sp. A of Matsuoka 1983, p. 130.)

Dimensions. Central body length (including apical horn) 45–53 μm , width 37–45 μm , wall thickness 2 μm ; process length 10–13 μm (Mao Shaozhi 1989).

Biological affinity. Unknown.

Intraspecific morphotypes. None.

Comparison. This species can be distinguished from all similar *Spiniferites* and *Achomosphaera* species by the unique, dense granules covering the wall and processes, its thick outer wall and brown colour (Mao Shaozhi 1989).

Remarks. Mao Shaozhi (1989) considered *Achomosphaera granulata* the same as *Achomosphaera* sp. A of Matsuoka 1983 from the Lower to Upper Miocene of the Niigata district, central Japan: but we disagree with this assessment; see also Londeix et al. (2018).

The species has been recorded only in Quaternary sediments of the South China Sea by Mao Shaozhi (1989) and Mao Shaozhi & Harland (1993). Londeix et al. (2018) considered this species to belong to *Hafniasphaera*; others, including KNM and VP were not convinced because the published holotype images are not sharp and the description does not mention the presence of vacuoles.

2.5. *Achomosphaera ramosasimilis* (Yun Hyesu 1981) Londeix et al. 1999

Synonymy. *Achomosphaera ramulifera* subsp. *ramosasimilis* Yun Hyesu 1981, p. 14–15, pl. 1, figs. 1, 8; text-fig. 3b.

Spiniferites ramuliferus (auct. non Deflandre) Reid; Reid 1974, p. 608, pl. 4, figs. 39–40.

Holotype. Yun Hyesu 1981, pl. 1, fig. 1; text-fig. 3b; Fensome et al. 1991, figs. 1–2, p. 719; fig. 4, p. 719 & 721 [initially described in German by Yun Hyesu 1981, translated by Fensome et al. 1991].

Type locality. Timmermann brickyard, new pit, near Esbeck, Westphalia, Germany.

Type stratum. Santonian, Upper Cretaceous (Yun Hyesu 1981).

Etymology. In reference to the close similarity between this species and *Spiniferites ramosus* (Fensome et al. 1991, p. 721).

Distinguishing characters. Thick-walled ovoid to spheroidal central body with a granular or smooth pedium and a smooth tegillum bearing hollow, distally closed, exclusively gonal processes. The processes on the cingulum may be connected by crests, similar to some processes in the apical and antapical areas. There is always a thin apical process, occasionally with a terminal hooklet. Sutures can be partly present. The archeopyle is formed by the loss of plate 3". (Based on Yun Hyesu 1981, p. 14–15) and Fensome et al. 1991, p. 719–720.)

Dimensions. Central body length 30 (32) 36 μm , width 32 (39) 42 μm ; maximum length of processes 16–18 μm (Yun Hyesu 1981).

Biological affinity. Unknown.

Intraspecific morphotypes. None.

Comparison. According to Yun Hyesu (1981), because *Achomosphaera ramosasimilis* possesses a thick wall, partial presence of sutures, does not have all processes connected by crests, bears a simple apical process and no antapical branched process, it differs from *Achomosphaera ramulifera*.

Remarks. This species was observed by Londeix et al. (1999) from the Lower Pliocene of the Strait of Sicily, central Mediterranean Sea. LL also considers specimens of "*Spiniferites ramuliferus*" described by Reid (1974) from recent raised-beach deposits at Woodgrange, Northern Ireland, U.K. to be probably *Achomosphaera ramosasimilis* and not *Achomosphaera ramulifera*; see discussion in Londeix et al. (2018) and Gurdebeke et al. (2018).

2.6. *Spiniferites alaskensis* Marret et al. 2001 ex Marret in Fensome & Williams 2004

Synonymy. None.

Holotype. Marret et al. 2001, pl. 1, figs. 7–9, designated by Marret in Fensome & Williams (2004).

Type locality. ODP Site 887, Gulf of Alaska, northeastern North Pacific, Gulf of Alaska.

Type stratum. Marine Isotope Substage 5e; Sample 887B-2H-5, 65 cm (Marret et al. 2001).

Etymology. Named *alaskensis* from the type locality (Marret et al. 2001).

Distinguishing characters. Ovoid shape with an apical boss. The cyst wall is thin (< 1 μm) and has a finely granulate to scabrate surface. Processes are gonal and relatively broad (2 μm), each process terminating in a simple trifurcation with pointed ends. Low sutural septa are present between processes and define a gonyaulacacean tabulation. The archeopyle is formed by loss of plate 3". (Based on Marret et al. 2001, p. 384–385.)

Dimensions. Central body length 26.3 (31.4) 36.8 μm , width 23.6 (29.3) 31.5 μm ; process length 7.5 (10.1) 12.5 μm (Marret et al. 2001).

Biological affinity. Unknown.

Intraspecific morphotypes. None.

Comparison. This species differs from other *Spiniferites* species only by the process shape and termination. *Spiniferites alaskensis* has broad processes with simple, short, trifurcate branches with pointed ends; such processes are unusual for late Quaternary *Spiniferites* species (Marret et al. 2001, p. 386).

Remarks. The name was validated by Marret in Fensome & Williams (2004) because Marret et al. (2001) did not indicate which of the illustrations represented the holotype. This species is discussed in Marret & Mertens (2018).

2.7. *Spiniferites asperulus* Matsuoka 1983 (Plate 3, figures 1–6)

Synonymy. None.

Holotype. Matsuoka 1983, pl. 12, fig. 2.

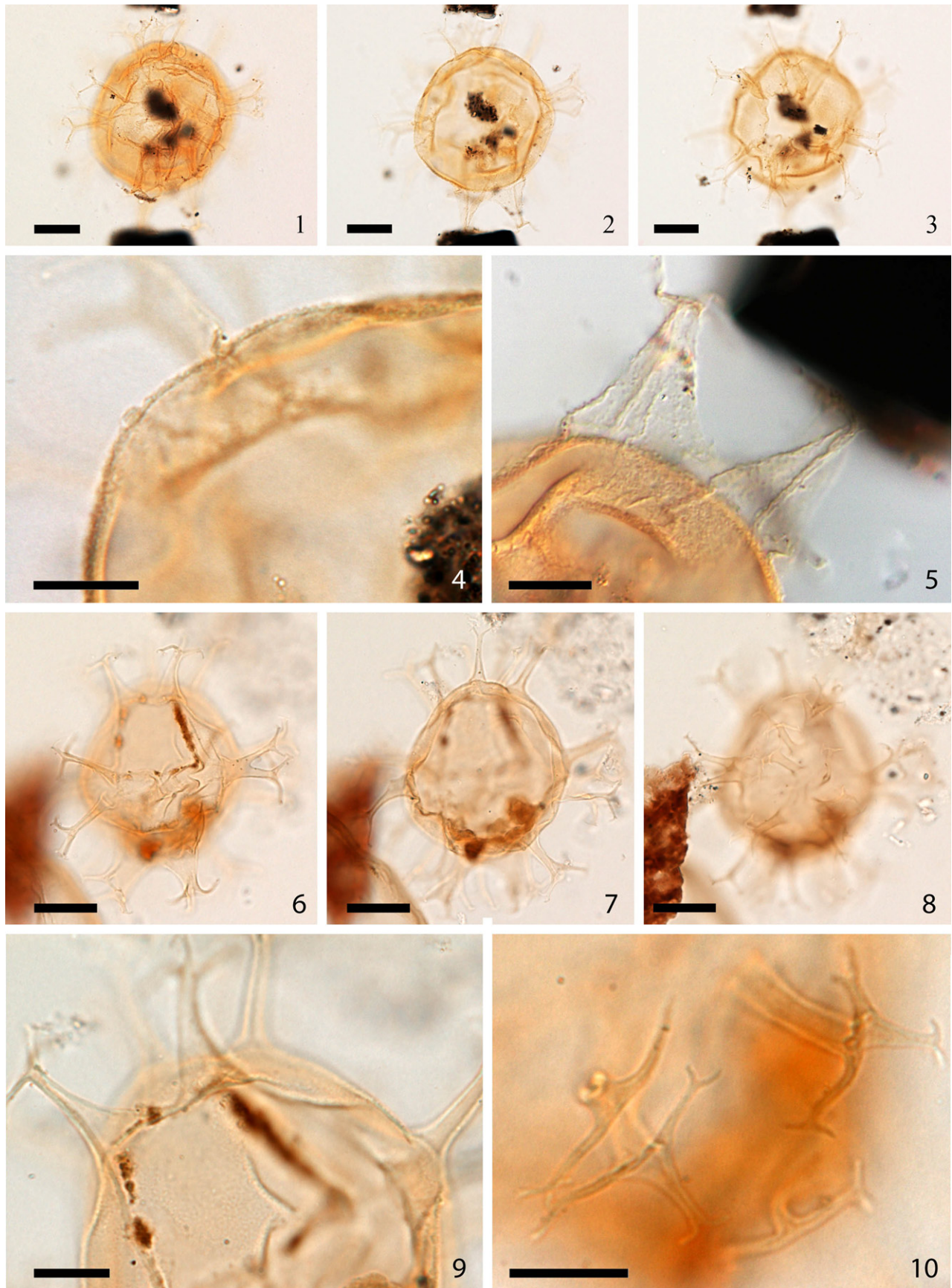


Plate 3. 1–3. Holotype of *Spiniferites asperulus* Matsuoka 1983 in ventral view at high to low focus. 4. Same specimen, mid-focus showing wall structure. 5. Same specimen, mid-focus showing antapical processes. 6–8. Holotype of *Spiniferites firmus* Matsuoka 1983 in ventral view at high to low focus. 9. Same specimen, showing microgranular wall. 10. Same specimen, showing distal ends of cingular processes. Slides provided by KM, photographed by KNM. All scale bars = 10 μ m, except 1–3, 7–9 = 20 μ m.

Type locality. Nishiyama, Nishiyama-cho, Niigata Prefecture, Central Japan.

Type stratum. Nishiyama Formation, Pliocene or younger (Matsuoka 1983).

Etymology. From the Latin, *asper* (somewhat rough), in reference to the coarsely granular surface of the cyst (Matsuoka 1983, p. 131).

Distinguishing characters. The subspheroidal to ovoid cyst has a relatively thick wall. The tegillum forms many small invaginations in the intratabular area. No granules are present. The processes are slender, membranous, gonal (and occasionally intergonal?) and widen at the base; the two antapical processes are somewhat more robust and connected by a slightly elevated crest. (Based on Matsuoka 1983, p. 131–132, and observations by KNM.)

Dimensions. Central body length 48–69 µm, width 45–64 µm; process length up to 16 µm (Matsuoka 1983).

Biological affinity. Unknown.

Intraspecific morphotypes. None.

Comparison. The wall structure is similar to that of *Spiniferites ludhamensis*, but there are many more invaginations in *Spiniferites asperulus*, and *Spiniferites ludhamensis* is smaller (central body length, 38–49 µm) and has completely hollow processes. *Spiniferites membranaceus* has a granular wall.

Remarks. LL expressed the difficulty in differentiating this species from others, such as *Spiniferites firmus*. KM stated that, after having described it back in 1983, he now has no clear recollection of what this species is. LL looked at the holotype, but adds that he did not look at the total population and therefore finds it hard to say if this is a distinct species or not. He noted that granulation, which may occur as a variation in many species, could be a response to specific environmental conditions. The original description mentions the occasional occurrence of intergonal processes, a feature confirmed by KM. This species is discussed in Limoges et al. (2018).

2.8. *Spiniferites belerius* Reid 1974

Synonymy. Non *Spiniferites belerius* sensu Harland 1977, p. 98–99, pl. 1, figs. 7–10, pl. 2, figs. 7–10, 16–21, 25–57 [= *Spiniferites membranaceus*].

Holotype. Reid 1974, pl. 2, figs. 12–13.

Type locality. Severn Estuary, England, U.K.

Type stratum. Modern surface sediments (Reid 1974).

Etymology. From the Latin, *belerium*, which is the Roman name for the promontory on which Land's End, Cornwall, England, is situated (Reid 1974, p. 596).

Distinguishing characters. The small central body is oval, with a finely granular wall and an apical boss. The processes are gonal and connected by low crests with a typical process shape. This species was described as having a characteristic large 'trumpet-shaped' posterior process at the junction of plates 1 and 2 (Reid 1974, p. 597; but see Gurdebeke et al. 2018).

Dimensions. Central body length 35–42 µm, width 28–37 µm; maximum process length 7–10 µm, posterior process length 10–15 µm (Reid 1974).

Biological affinity. *Gonyaulax scrippsae* Kofoid 1911 as depicted by Wall & Dale (1968, p. 270, pl. 1, fig. 14) according to Reid (1974). LL and KZ noted some similarity to the cyst of *Gonyaulax baltica* Ellegaard, Lewis & Harding 2002, as produced in batch-cultures and illustrated by Ellegaard et al. (2002). KZ felt she could not understand the cyst-based species concept here because of the large morphological variation documented in that study. VP wondered if anyone could distinguish cysts of *Gonyaulax baltica* in the sediments. ME replied that some cysts of *Gonyaulax baltica* could be the same as *Spiniferites belerius*, but ideally we should first derive *Spiniferites belerius* in culture and compare the phylogenetics.

Intraspecific morphotypes. None.

Comparison. LL noted during the first workshop that *Spiniferites bentorii* is larger overall and has a hypocyst larger than the epicyst. *Spiniferites belerius* is similar to *Spiniferites coniconcavus*, but the latter has wider process bases.

Remarks. During the first and second workshops there was agreement that this species is problematic. LL considered this species as having a large morphological variation. He also suggested that this species is defined by central body size and shape and the presence of short processes that are not well developed in the apical region. PJM mentioned that specimens from the Black Sea show a very wide morphological range and that these could be used as an illustration of the species' various morphologies. KNM stated, however, that potentially different species have been described as *Spiniferites belerius* given the great variation that he has observed globally. PJM remarked that this is hard to tell without culture studies. LL proposed that two categories be defined for practical purposes: typical and atypical morphotypes. These categories can then be used in paleoecological studies. LL further underlined the wide range in morphology that appears to characterise many Paratethyan species. PJM asked LL whether he considered *Spiniferites belerius* to be Paratethyan, and LL answered "no". He noted that there is a clear regular shape, and a wide range of morphological variability, and that it is sometimes hard to know if this represents infraspecific variability or more than one species. When PJM asked what LL considers a Paratethyan species, he replied that it is an "endemic" species with a clearly defined, typical morphology. He used *Serilodinium explicatum* Eaton 1996, *Invertocysta?* sp. A of Londeix et al. (2009), *Invertocysta?* sp. B of Londeix et al. (2009), *Pterocysta cruciformis* Rochon et al. 2003, *Pyxidinospis psilata* (Wall & Dale in Wall et al. 1973) Head 1994, *Galeacysta etrusca* Corradini & Biffi 1988 and *Caspidinium rugosum* Marret in Marret et al. 2004 as good examples of Paratethyan species. PJM commented in draft that LL's examples include taxa not recorded outside the Ponto-Caspian basins together with taxa having wide ranges from the saline western Mediterranean Sea to the brackish Aral Sea. She considers it difficult to justify the word endemic for such a broad grouping of taxa. She considers that by definition, an endemic species means native or restricted to a certain country or area and should not be used for Paratethyan forms as the Paratethys was a vast Euro-Asian waterway. BD suggested that we should decide whether we can put species into two different groups: those

that are stable and well-described, and those that originate from particular extreme environments that induce increased ecological pressure. He said that much of the discussion appears to be focused on forms from extreme environments. He noted, however, that he does not know how to apply such an approach in practice, but proposed that “weird” morphotypes should be addressed “later on”, once clear basic forms have been established. KNM suggested that the topotype material of *Spiniferites belerius* should be looked at to evaluate the morphological variability present. This has now been done by Gurdebeke et al. (2018). Limoges et al. (2018) have accepted the presence of additional intergonal processes in this species.

2.9. *Spiniferites bentorii* (Rossignol 1964) Wall & Dale 1970

Synonymy. *Hystrichosphaera bentorii* Rossignol 1964, p. 84–85, pl. 1, figs. 3, 3 inset, 5–8; pl. 3, figs. 2–3; text-figs. A–F.

Leptodinium churchillii Harland 1968, p. 548, 550–551, figs. 12–13, 22–24.

non *Spiniferites nodosus* (Wall 1967) Sarjeant, 1970. [Synonymy proposed by Reid (1974, p. 599) is here rejected.]

non *Spiniferites bentorii* sensu Wall & Dale 1970, p. 52, pl. 1, figs. 26, 28.

Holotype. Rossignol 1964, pl. 1, figs. 3, 7–8.

Type locality. Ashdod borehole, coastal plain, Israel.

Type stratum. Quaternary sediments, 172–172.5 m depth (Rossignol 1964).

Etymology. Named after Dr. Yaakov Ben-Tor (b. 1910 – d. 2002), Israeli geologist who was head of the Israeli Geological Survey at the time of Martine Rossignol’s study and provided her with samples.

Distinguishing characters. This species typically has a pear-shaped central body with a characteristic apical boss. It bears characteristic tapering, slender, gonol and occasionally intergonal processes, with the two antapical processes being the longest. The process bases may be fenestrate. Sutures are marked by low ridges, and sometimes vacuoles are present in the sutures. The wall is smooth to microgranular. The cingular displacement is relatively large (three times its width according to Reid 1974; one and a half to two times its width according to Wall 1965). Tabulation is typical for the genus according to Wall (1965) and Harland (1968), with four apical plates, although the suture between 1’ and 2’ is faint and was not observed by Rossignol (1964) or Price & Pospelova (2014), both interpreting this as indicating the presence of only three apical plates visible on the cyst. The sulcus is often well expressed and straight, and widens posteriorly (Reid 1974). The archeopyle is formed by loss of plate 3” and is reduced with rounded corners. (Based on Rossignol 1964, p. 84–85, Harland 1968, p. 542–543, Reid 1974, p. 598–600, Rochon et al. 1999, p. 34, Price & Pospelova 2014, p. 13, and observations of the participants). MJH noted in draft that specimens from the Last Interglacial of the Baltic have distinctive lateral cingular processes in which the distal furcations branch abruptly at 90° to the process shafts

and point towards both poles (Head 2007, fig. 7j,k,m). MJH further noted in draft that specimens of *S. bentorii* that he has observed have archeopyles well defined by the sutures.

Dimensions. Central body length 60–73 µm, width 45–63 µm; process length 15–20 µm (25 µm for the antapical processes) (Rossignol 1964). Central body length 58–69 µm, width 52–55 µm; length of processes 0–20 µm (Reid 1974).

Biological affinity. *Gonyaulax digitale* (Pouchet 1883) Kofoid 1911 according to Wall & Dale (1967, p. 352) and Dodge (1989, p. 283).

Intraspecific morphotypes. Rossignol (1964) erected *Hystrichosphaera bentorii* var. *truncata* to encompass specimens with shorter processes. This variety later was transferred, along with the species, to *Spiniferites* (Lentin & Williams 1973). *Spiniferites bentorii* var. *globus* Morzadec-Kerfourn 1979, p. 222–224, pl. 31, fig. 10, was introduced to encompass specimens with a spheroidal central body, a smaller apical boss, and longer, more slender processes. Several subspecies have been described from the Neogene deposits of the Pannonian Basin in central Europe, of which four were validly published: *Spiniferites bentorii* subsp. *budajenoensis* Sütő-Szentai 1986, *Spiniferites bentorii* subsp. *granulatus* Fuchs & Sütő-Szentai 1991, *Spiniferites bentorii* subsp. *oblongus* Sütő-Szentai 1986 (now *Spiniferites oblongus* Soliman & Riding 2017), and *Spiniferites bentorii* subsp. *pannonicus* Sütő-Szentai 1986. Another four were proposed but not validly published: “*Spiniferites bentorii* subsp. *coniunctus*” Sütő-Szentai 1990, “*Spiniferites bentorii* subsp. *matraensis*” Sütő-Szentai 1988, “*Spiniferites bentorii* subsp. *piriformis*” Sütő-Szentai 1988, and “*Spiniferites bentorii* subsp. *pseudooblongus*” Sütő-Szentai 1983. None of the eight morphotypes have been recorded from Pliocene–Quaternary sediments.

Comparison. *Spiniferites bentorii* is similar to *Spiniferites lazus* in that it can have fenestrate process bases, but is distinguished from *Spiniferites lazus* by its larger size, pear-shape (as opposed to elongate-ovoid), ambitus, process form, and cingulum displacement (Reid 1974). According to Rochon et al. (1999), the central body of *Spiniferites bentorii* can be ovoid, but herein we assign such ovoid forms to *Spiniferites lazus*. *Spiniferites bentorii* differs from *Spiniferites multisphaerus* on the basis of its wall structure, which does not contain vacuoles, unlike *Spiniferites multisphaerus* (Price & Pospelova 2014). *Spiniferites hainanensis* has an ovoid central body. For *Spiniferites nodosus*, see Section 2.26.

Remarks. During the first workshop, VP pointed out that *Spiniferites bentorii* can have intergonal processes: specimens illustrated by Price & Pospelova (2014) corresponding to *Spiniferites bentorii* subsp. *truncatus* show such processes. Rochon et al. (1999) also mentioned the presence of occasional intergonal processes in this species. LL remarked that the presence of intergonal processes is not a problem at the species level if they are rare or sparse, and there is no more than one between adjacent gonol processes. LL further remarked that he does not consider the apical boss an important characteristic, but that the pear-shaped central body is important. Wall & Dale (1970), while transferring

Hystrichosphaera bentorii Rossignol to the genus *Spiniferites*, illustrated a morphotype that does not conform to our understanding of the species. This morphotype (Wall & Dale 1970, p. 52, pl. 1, figs. 26, 28) bears at least two intergonal processes between pairs of gonal processes, and, despite the presence of an apical boss, we consider it equivalent to *Spiniferites hyperacanthus*. KNM remarked that the cyst-defined plate formula originally provided by Rossignol (1964) is incorrect since all specimens she studied show four apical plates and not three. The species is further discussed by Limoges et al. (2018), who report the occasional presence of intergonal processes.

2.10. *Spiniferites bulloideus sensu Wall (1965)*

Synonymy. *Hystrichosphaera bulloidea* auct. non Deflandre & Cookson 1955; Wall 1965, fig. 6; Wall & Dale 1967, pl. 1, fig. K; Wall & Dale 1968, pl. 1, figs. 14–15. non *Spiniferites ramosus sensu Wall & Dale 1970*, pl. 1, figs. 14–15 [in contrast with Harland 1977, p. 102]. non cyst of *Gonyaulax* sp. aff. *Gonyaulax spinifera* (= *Spiniferites ramosum* [sic]) in Wall 1971, pl. 2, fig. 4 [in contrast, Harland 1977, p. 102 considered this a possible synonym].

Holotype. Not relevant.

Type locality. Not relevant, but initially described by Wall (1965) from coastal waters off Woods Hole, MA, USA (also from the same locality by Wall & Dale 1967, 1968, 1970).

Type stratum. Not relevant.

Etymology. Not relevant.

Distinguishing characters. Ovoid central body without an apical boss and bearing exclusively gonal processes. The two antapical processes are longest, membranous and of more or less equal width. There may be extensive development of crests between the processes. The cingulum is displaced. The tabulation is typical for the genus, 3–4' (suture between 1' and 4' faintly visible), 0a, 6', 6c, 5–6', 1p, 1'. (Based on Wall 1965, p. 300–302, Wall & Dale 1968, p. 270, and observations recorded here.)

Dimensions. Central body length 30–40 µm (Wall 1965) and 32–42 µm (Wall & Dale 1968), width 28–39 µm; process length up to 16 µm (Wall & Dale 1968).

Biological affinity. Related to *Gonyaulax scrippsae* by Wall & Dale (1967, p. 352; 1968, p. 270). Ellegaard et al. (2002, p. 783) recorded cysts of *Gonyaulax baltica* “similar to *Spiniferites bulloideus sensu Wall & Dale 1968*” in addition to *Spiniferites belerius* (see remarks therein). The relationship between *Gonyaulax baltica* and the respective cyst-based species needs further study.

Intraspecific morphotypes. None.

Comparison. *Spiniferites belerius* differs from *Spiniferites bulloideus sensu Wall (1965)* in that *Spiniferites belerius* has an apical boss. *Spiniferites bulloideus sensu Wall (1965)* differs from *Spiniferites falcipedi* in being much smaller, and from *Spiniferites pacificus* in not having intergonal processes. The two antapical tubular processes distinguish this form from *Spiniferites ramosus sensu Rochon et al. (1999)*.

Remarks. Specimens Wall (1965) attributed to *Spiniferites bulloideus* were recovered from coastal waters off Woods Hole, MA, USA, and later reported by Wall & Dale (1967, 1968, 1970) from the same locality. All these studies considered the specimens to belong to *Spiniferites bulloideus sensu stricto*. However, Harland (1977, p. 102) and later Head (1996a, p. 1205) remarked that “*Spiniferites bulloideus sensu Wall 1965*” (and later referred to by Wall & Dale 1967, 1968) is a distinctive form that should not be attributed to neither *Spiniferites bulloideus sensu stricto* nor *Spiniferites ramosus*. *Spiniferites bulloideus sensu stricto* was first described by Deflandre & Cookson (1955, as *Hystrichosphaera bulloidea*, pl. 5, figs. 3–4, from the Middle Miocene of Balcombe Bay, Victoria, Australia (as mentioned in Deflandre & Cookson 1955, caption to pl. 5, figs. 3–4). It can be described as having a small, spheroidal central body (length 30–37 µm) with a thin, delicate wall bearing slender processes 10–15 µm long that are probably gonal as well as intergonal (based on Deflandre & Cookson 1955, p. 264, and our observations). The etymology was not specified by the authors, but is presumably derived from the Latin *bulla* (bubble) and the Greek *oides* (resembling), in reference to the spheroidal central body resembling a bubble. According to Deflandre & Cookson (1955), *Hystrichosphaera bulloidea* (now *Spiniferites bulloideus*) differs from *Hystrichosphaera furcata* (now considered a synonym of *Spiniferites ramosus*) in general outline, dimensions, and the nature of the processes, and from *Hystrichosphaera ramosa* (now *Spiniferites ramosus*) by its spheroidal central body, smaller size and generally more slender processes. During the first round-table discussion, participants expressed uncertainty as to whether Quaternary specimens designated as *Spiniferites bulloideus* (e.g., Reid 1974, figs. 17–19; Turon & Londeix 1988, pl. 1, figs. 10–12; McMin 1991, pl. 2, figs. 7, 12) are conspecific with the holotype of Deflandre & Cookson (1955). LL added a note after the first workshop that he considered the specimen illustrated by Turon & Londeix (1988, pl. 1, figs. 10–12) as a good example of *Spiniferites bulloideus sensu stricto*. KNM, however, remarked that Deflandre & Cookson’s specimen has a different orientation than Turon & Londeix’s (1988) specimen, which was shown in apical and antapical views; so there is some uncertainty as to whether it belongs to *Spiniferites bulloideus* since we cannot confirm if the central body is completely spheroidal. The same situation is true for images shown by McMin (1991, pl. 2, figs. 7, 12). During the first round-table discussion, there was more or less agreement that *Spiniferites bulloideus sensu stricto* could be synonymous with *Spiniferites ramosus*, possibly as a subspecies. The synonymy of *Spiniferites ramosus* with *Spiniferites bulloideus* was previously proposed by Harland (1977) and accepted by Matsuoka (1987a). In either case, the holotype should be rephotographed, but since the type material is in Australia there was no immediate possibility to do this. Either way, as BD expressed during his presentation at the second workshop and followed here, *Spiniferites bulloideus sensu Wall 1965* is different from *Spiniferites bulloideus sensu stricto*, based on the fact that it has two strong antapical processes, tubular processes, and no intergonal processes or

membranous developments. KNM added that the central body of *Spiniferites bulloideus* sensu Wall 1965 is not spheroidal.

2.11. *Spiniferites coniconcavus* De Schepper et al. 2004

Synonymy. *Spiniferites* sp. 1 of Louwye et al. 2004, figs. 7r–t.

Holotype. De Schepper et al. 2004, p. 628, figs. 5.1–5.20.

Type locality. Verrebroek Dock, northern Belgium.

Type stratum. Basal Shelly Unit, Lillo Formation; upper Lower Pliocene (De Schepper et al. 2004).

Etymology. From the Latin, *conus* and *concavus*, in reference to the principal processes, whose bases are cone-shaped with concave sides (De Schepper et al. 2004).

Distinguishing characters. Broadly ovoid central body bearing gonal processes only. Process stems are hollow, broad and conical with concave sides near the base, distally becoming cylindrical and narrower; closed distally with short and blunt, usually trifurcate endings. Tabulation expressed by low sutural crests and archeopyle is formed by loss of plate 3". Operculum is free. (Based on De Schepper et al. 2004, p. 628.)

Dimensions. Central body length 38 (39.9) 40 µm, width 34 (35.0) 36 µm; process length 7 (9.8) 12.5 µm, width of process base 4.0 (6.8) 9.0 µm, width of process tip 1.0 (1.7) 2.0 µm (De Schepper et al. 2004).

Biological affinity. Unknown.

Intraspecific morphotypes. None.

Comparison. *Spiniferites belerius* differs in having an apical boss. *Spiniferites bulloideus* sensu Wall 1965 has trifurcate process terminations that bifurcate distally, in contrast to the blunt and reduced process terminations of *Spiniferites coniconcavus*.

Remarks. During the first workshop, LL wondered how the specimens illustrated in De Schepper et al. (2004, figures 5.17–20) differ from *Spiniferites belerius*. SD replied that the process bases are wider. This species is further discussed by Gurdebeke et al. (2018).

2.12. *Spiniferites cruciformis* Wall and Dale in Wall et al. 1973

Synonymy. None.

Holotype. Wall et al. 1973, pl. 1, figs. 2–3.

Type locality. Black Sea, Core 1451G.

Type stratum. Lower Holocene sediments; 66.5 cm (Wall et al. 1973).

Etymology. From the Latin, *cruci-* (stem of *crux*, cross) and *-form*, in reference to the shape of the central body.

Distinguishing characters. Large cysts with characteristic cruciform shape, moderately dorsoventrally compressed, with sutural septa of variable height that may be perforated (Wall et al. 1973, p. 21–22).

Dimensions. Central body length 46–65 µm, width 34–56 µm, depth ~28 µm; process length up to 28 µm (Wall et al. 1973).

Biological affinity. Unknown.

Intraspecific morphotypes. Different morphotypes have been described by Mudie et al. (2001; 2018) and Marret et al. (2004). In the Caspian Sea, morphologies with an elongated apical boss are included in the species by Marret et al. (2004), whereas the holotype and most of the Black Sea morphologies have a rounded apex.

Comparison. This species is easily distinguishable from all other species of *Spiniferites* by its flattened cruciform shape, with strongly concave sides above and below the cingulum in equatorial view (Wall et al. 1973).

Remarks. *Spiniferites cruciformis* was first described by Wall & Dale in Wall et al. (1973) from the Lower Holocene of the Black Sea. PJM added a note after the workshop that there is agreement among herself, AR, LL and Shannon Ferguson that the species *Spiniferites cruciformis*, *Pterocysta cruciformis* and *Galeacysta etrusca* belong to separate genera and do not intergrade; AG notes during drafting that he agrees. This species and related taxa are further discussed by Mudie et al. (2018), who provide definitions for the terms cruciform, galeate and pterate, as well as a table of characteristics distinguishing these and other taxa grouped in the so-called *Galeacysta etrusca* complex of Popescu et al. (2009). MJH in draft provided the following information: Although preserved as a single grain mount, the holotype is desiccated making any detailed observations impossible.

2.13. *Spiniferites delicatus* Reid 1974

Synonymy. None.

Holotype. Reid 1974, pl. 2, figs. 20–22.

Type locality. Dee Estuary, England, U.K.

Type stratum. Modern surface sediment (Reid 1974).

Etymology. In reference to the delicate sutural membranes joining the processes (Reid 1974).

Distinguishing characters. Central body ovoid with microgranular inner and outer wall layers. An apical node or low boss may be present at the anterior end of 1' and 4'. Processes are membranous and exclusively gonal, with petaloid process tips. High sutural crests connect the processes. Both processes and crests have microgranular surfaces. The cingulum is sinistral and displaced by three times its width. The tabulation is typical for the genus, with an apical series of four plates; sulcal plates are visible. The archeopyle is formed by loss of plate 3". (Based on Reid 1974, p. 601–602, and Rochon et al. 1999, p. 34.)

Dimensions. Central body length 40–60 µm, width 35–54 µm; cingulum width 6–9 µm; maximum process length 29 µm (Reid 1974).

Biological affinity. Unknown, but probably *Gonyaulax* sp., according to Rochon et al. (1999).

Morphotypes. None.

Comparison. *Spiniferites delicatus* has processes of similar shape to *Spiniferites ristingensis* but connected by high sutural crests, and a central body wall structure characterised by a pedium with radial fibers and a thin granular tegillum whose surface appears microgranular to microreticulate. *Spiniferites delicatus* also differs in having a reduced archeopyle.

Remarks. During the first workshop several participants wondered how to differentiate this species from *Spiniferites ristingensis*. Everybody agreed that the holotype of *Spiniferites delicatus* should be reinvestigated. LL gave some examples of specimens he considers typical *Spiniferites delicatus* (see Londeix et al. 2018). FM stressed the importance of the more elaborate development of the crests in *Spiniferites delicatus*. There was overall agreement during the second workshop that the so-called “skeletal rods”, as first described by Reid (1974), do not exist and are an optical illusion created by the attachment of membranes along the processes. This species is further discussed by Gurdebeke et al. (2018).

2.14. *Spiniferites elongatus* Reid 1974

Synonymy. Resting spore of *Gonyaulax* sp. 1. Wall & Dale, 1968, pl. 1 fig. 16 [fide Reid 1974].

cf. *Hystrichosphaera* sp. a. Harland & Downie 1969, p. 232, pl. 7 fig. 4 [fide Reid 1974].

Spiniferites ellipsoideus Matsuoka 1983, p. 132–133, pl. 13 figs. 6–7.

Spiniferites frigidus Harland & Reid in Harland et al. 1980, p. 213–216, fig. 2A–J.

Rottnestia amphicavata Dobell & Norris in Harland et al. 1980, p. 218–220, fig. 4A–N.

Rottnestia amphicavata var. B. Dobell & Norris in Harland et al. 1980, p. 220–222, fig. 4O–P, fig. 8A–E, J–P.

Rottnestia amphicavata var. C. Dobell & Norris in Harland et al. 1980, p. 222, fig. 8F–I, Q, R.

Spiniferites cf. *elongatus*. Harland & Sharp 1986, pl. 1 figs. 9–16.

Holotype. Reid 1974, pl. 3, figs. 23–24.

Type locality. Estuary of the River Ythan, Scotland, U.K.

Type stratum. Modern surface sediments (Reid 1974).

Etymology. From its characteristic elongate shape (Reid 1974).

Distinguishing characters. Central body elongate and ellipsoidal with a smooth to finely microgranulate surface and no apical boss. Sutural crests are membranous and hollow with varying height, being low around the cingulum and high on the hypocyst and towards the apex. Processes are exclusively gonial. The cingulum is displaced by less than one to two times its width. Tabulation is typical for the genus. Sulcal plates are weakly expressed and the sulcus is aligned parallel to the longitudinal axis, increasing to three times its anterior width posteriorly. Plate 6” is triangular, long and narrow. The archeopyle is formed by loss of plate 3” and reduced. (Based on Reid 1974, p. 602–603, Rochon et al. 1999, p. 34–36, Van Nieuwenhove et al. 2018, and Gurdebeke et al. 2018.)

Dimensions. Central body length 40–59 µm, width 26–42 µm; wall thickness 0.8–1 µm; apical process length 6–12 µm, antapical process length 12–16 µm, lateral process length 9 µm (Reid 1974).

Biological affinity. Reid (1974) associated *Spiniferites elongatus* with *Gonyaulax scrippsae*, following observations by Wall & Dale (1968); Rochon et al. (1999) associated it with

Gonyaulax spinifera. Ellegaard et al. (2003) found the motile stage of *Spiniferites elongatus* to represent an undescribed species of *Gonyaulax*, and using a unified approach to cyst and motile stage taxonomy/nomenclature, transferred *Spiniferites elongatus* to the genus *Gonyaulax*, as *G. elongata* (Reid 1974) Ellegaard et al. 2003. The present report follows the prevailing practice among cyst researchers of using dual taxonomy/nomenclature (Head et al. 2016; but see Ellegaard et al. 2018), and hence the name *Spiniferites elongatus* is here retained.

Intraspecific morphotypes. *Spiniferites* cf. *elongatus* of Harland & Sharp (1986). These cysts were recovered from surface sediments of the Norwegian Sea, and differ from *Spiniferites elongatus* in being “smaller and slightly less membranous. They are more compact, and the processes are shorter and can appear as squat and somewhat ‘dumpy’ structures, especially on the dorsal surface” (Harland & Sharp 1986). These forms are now considered part of the morphological spectrum of *Spiniferites elongatus*, and can be informally referred to as *Spiniferites elongatus* – Norwegian morphotype, as noted in Van Nieuwenhove et al. (2018). Although the height of sutural crests and their degree of development is variable in *Spiniferites elongatus*, they are less elaborately developed in typical specimens of *Spiniferites elongatus* (sensu Reid 1974) than in *Rottnestia amphicavata* or *Spiniferites frigidus*, and individual processes are more prominent (Rochon et al. 1999). However, Van Nieuwenhove et al. (2018) illustrate a morphological continuum and lack of clear cut-off criteria to distinguish *Spiniferites frigidus* from *Spiniferites elongatus*, and that the features of *Rottnestia amphicavata* used to place it in this genus can be accommodated in *Spiniferites*. Hence, *Rottnestia amphicavata* and *Spiniferites frigidus* are also considered junior synonyms of *Spiniferites elongatus* by Van Nieuwenhove et al. (2018). They further suggest that the “flamboyant” membrane morphology formerly encompassed by *Rottnestia amphicavata* and *Spiniferites frigidus* be can informally referred to as *Spiniferites elongatus* – Beaufort morphotype.

Comparison. *Spiniferites elongatus* is differentiated from all other species of *Spiniferites* by its elongate shape.

Remarks. *Spiniferites ellipsoideus* was first described by Matsuoka (1983) from Middle to Upper Miocene river cliff sediments of Shin-shinanogawa, Teradomari-cho, Niigata Prefecture, central Japan. During the first workshop, participants expressed the opinion that this species is likely a junior synonym of *Spiniferites elongatus*, but that the type assemblage should be checked. KM remarked in a personal communication to KNM that “This elongate cyst is similar to modern *Spiniferites elongatus*, but *Spiniferites ellipsoideus* is smaller than *Spiniferites elongatus* and with less development of the antapical membrane. I think *Spiniferites ellipsoideus* is an independent species from *Spiniferites elongatus*”. KNM remarked in draft that measurements reported by Matsuoka (1983) (length of 36–49 µm, width of cyst 24–33 µm, and length of processes up to 13 µm) do not allow an unambiguous differentiation from measurements reported for *Spiniferites elongatus* by Reid (1974) and Ellegaard et al. (2003); this is confirmed by new measurements provided by Van Nieuwenhove et al. (2018) who therefore

recommend treating *Spiniferites ellipsoideus* as a junior synonym of *Spiniferites elongatus*. For *Spiniferites frigidus* and *Rottnestia ampicavata* see also Van Nieuwenhove et al. (2018).

2.15. *Spiniferites falcipedi* Warny & Wrenn 1997

Synonymy. *Achomosphaera* sp. in Head 1997, p. 171, figs. 4.12–4.16, 15.10, 15.11.

Holotype. Warny & Wrenn 1997, pl. 5, figs. 1–4.

Type locality. Bou Regreg S Core, Salé, Riffian Corridor, Morocco.

Type stratum. Messinian (Warny & Wrenn 1997).

Etymology. From the Latin, *falcipedi*, meaning bow legs, in reference to the wide antapical processes that arise from a common suturocavate base (Warny & Wrenn 1997).

Distinguishing characters. Central body spheroidal to slightly elongate with a microgranular to granular outer wall, bearing exclusively gonial, large, membranous, hollow processes. The essential criteria for this species are the wide antapical processes connected by a generally high flange (the so-called bow legs). A smaller process may arise from the flange connecting the two large antapical processes. The cingulum is offset by a distance equal to the width of the cingulum. (Based on Warny & Wrenn 1997, p. 291–297.)

Dimensions. Central body length 51.0–74.8 µm, width 47.6–64.6 µm, process length 10.2–25.5 µm (Warny & Wrenn 1997).

Biological affinity. Unknown.

Intraspecific morphotypes. None.

Comparison. *Spiniferites falcipedi* is similar to *Spiniferites mirabilis* but differs in having wide, exclusively gonial processes (Warny & Wrenn 1997). During the first workshop, LL pointed out the similarity between *Spiniferites falcipedi* and *Spiniferites pacificus*, although the latter has a much smaller central body (25.6–26.8 µm) and processes are not as wide; and it consistently bears intergonal processes. *Spiniferites strictus* is also smaller than *Spiniferites falcipedi* and has processes that are not as wide. *Spiniferites membranaceus* has a shorter central body, a higher flange, and a cingulum whose ends are offset by two cingulum widths. MJH added in draft that *Achomosphaera* sp. of Head (1997) from the Pliocene Coralline Crag of eastern England appears similar to *Spiniferites falcipedi* but is somewhat smaller, with a central body length of 46–55 µm (mean 49.4 µm) (Head 1997) compared with 51.0–74.8 (mean 54.7 µm) µm for *Spiniferites falcipedi* (Warny & Wrenn 1997). MJH also noted that the distal process branches on *Spiniferites falcipedi* are short, wide, flat, and solid whereas on *Spiniferites mirabilis* they are long, slender and tubular, and end in minute bifurcations.

Remarks. During the first workshop, there was a general comment that the holotype should be rephotographed, but this has not been possible.

2.16. *Spiniferites firmus* Matsuoka 1983 (Plate 3, figures 7–11)

Synonymy. None.

Holotype. Matsuoka 1983, pl. 14, figs. 5a–c.

Type locality. Hachioji, Oguni-cho, Niigata Prefecture, central Japan.

Type stratum. Haizume Formation, Lower Pleistocene (Matsuoka 1983).

Etymology. From the Latin, *firmus*, meaning stout, in reference to the stout processes (Matsuoka 1983).

Distinguishing characters. The cyst has a subspheroidal to ovoid central body, is characterised by a microgranular wall, and bears exclusively gonial, tapering, hollow processes with wide bases. The processes are connected by low sutures except between the two antapical processes, where the crest is elevated. The archeopyle is formed by loss of plate 3". (Based on Matsuoka 1983, p. 134; and observations of the holotype by KM, KNM and LL.)

Dimensions. Central body length 40–45 µm, width 38–50 µm; long processes 16–23 µm (Matsuoka 1983).

Biological affinity. Unknown.

Intraspecific morphotypes. None.

Comparison. This species is similar to *Spiniferites membranaceus*, but differs in having lower crests between the antapical processes and a larger central body. It also differs from *Spiniferites pachydermus* in possessing broader, tapering processes with wider bases. *Spiniferites firmus* differs from *Spiniferites pseudofurcatus* in having a smaller central body and processes without foliate distal extremities; it differs from *Spiniferites pseudofurcatus* var. *obliquus* in having no processes with a delicate, membraneous distal flare. According to Matsuoka (1983), *Spiniferites firmus* is most similar to *Spiniferites pacificus* and *Spiniferites falcipedi*, but those species have a smaller and a larger central body, respectively. In addition, *Spiniferites pacificus* has intergonal processes and *Spiniferites falcipedi* has wider processes.

Remarks. LL indicated in draft that the sutural features of this taxon are so faint that it could be considered to belong to *Achomosphaera*. At present it is retained in *Spiniferites*.

2.17. *Spiniferites hainanensis* Sun Xuekun & Song Zhichen 1992

Synonymy. None.

Holotype. Sun Xuekun & Song Zhichen 1992, pl. 1, fig. 12.

Type locality. Hainan Island, China.

Type stratum. Quaternary (Sun Xuekun & Song Zhichen 1992).

Etymology. Refers to the type locality, Hainan Island.

Distinguishing characters. The central body is slightly ovoid with a smooth to finely granular wall. It bears gonial and intergonal processes, connected by low perforated crests. The archeopyle is formed by the loss of plate 3". (Based on Sun Xuekun & Song Zhichen 1992, p. 49.)

Dimensions. Central body length 42.8–49.0 µm, width 35.0–42.0 µm; process length ~10.5 µm (Sun Xuekun & Song Zhichen 1992).

Biological affinity. Unknown.

Intraspecific morphotypes. None.

Comparison. Sun Xuekun & Song Zhichen (1992) noted that this species differs from all other known species of *Spiniferites* in having uniform perforations at the distal ends of the sutural ridges and one or two vacuoles in the middle part of each process; the latter provides the main criterion for distinguishing this species from *Spiniferites hyperacanthus*.

Remarks. This species is discussed further by Limoges et al. (2018).

2.18. *Spiniferites hexatypicus* Matsuoka 1983 (Plate 4, figures 1–4)

Synonymy. “*Spiniferites ovatus*” of Bujak 1984, pl. 3, figs. 15–18.

Holotype. Matsuoka 1983, pl. 13, figs. 1a–b.

Type locality. Teradomari, Teradomari-cho, Niigata Prefecture, central Japan.

Type stratum. Teradomari Formation, Middle to Upper Miocene (Matsuoka 1983).

Etymology. Derived from the Greek, *hexa* + *typicus* (hexagonal shaped), with reference to the hexagonal central body.

Distinguishing characters. The hexagonal central body lacks an apical boss. The wall surface is smooth to finely granular. The processes are exclusively gonial, short with simple or small bifurcate distal ends. (Based on Matsuoka 1983, p. 133–134.)

Dimensions. Central body length 62–71 µm, width 52–66 µm; process length up to 10 µm (Matsuoka 1983).

Biological affinity. Unknown.

Intraspecific morphotypes. None.

Comparison. According to Matsuoka (1983), this species is similar to *Spiniferites cingulatus* (now *Pterodinium cingulatum*) described from the Upper Cretaceous (Senonian), but differs in having a hexagonal central body and shorter processes. The length of the central body distinguishes this species from *Spiniferites ramosus* sensu Rochon et al. 1999.

Remarks. “*Spiniferites ovatus*” was invalidly published by Bujak (1984) because it is a junior homonym of *Spiniferites ovatus* Matsuoka 1983 [fide Bujak & Matsuoka 1986].

Spiniferites hexatypicus was recorded by Matsuoka (1983) from the Middle Miocene to Pliocene of Japan. It was also recorded by Mao Shaozhi & Harland (1993) from the Upper Pleistocene of the South China Sea. All workshop participants agreed that this is a poorly known species. LL considered it to fall within the morphological variability range of *Spiniferites ramosus*. KNM remarked in draft that the holotype is very compressed, and that the hexagonal shape could be an artefact as a result of compression.

2.19. *Spiniferites hyperacanthus* (Deflandre & Cookson 1955) Cookson & Eisenack 1974

Synonymy. *Hystrichosphaera hyperacantha* Deflandre & Cookson 1955, p. 264–265, pl. 6, fig. 7. non *Spiniferites* subsp. *multiplicatus* (Rossignol 1964, p. 86, pl. 1, fig. 14; pl. 3, fig. 16)

Lentin & Williams 1973, p. 130 [a synonym according to Matsuoka (1985, p. 35), but not accepted here].

Holotype. Deflandre & Cookson 1955, pl. 6, fig. 7.

Type locality. Balcombe Bay, Victoria, Australia.

Type stratum: Middle Miocene (Deflandre & Cookson 1955).

Etymology. Not specified by Deflandre & Cookson (1955), but presumably from the Greek *hyper* (excess, high degree) and *akanthos* (spine).

Distinguishing characters. Central body spheroidal with a well-expressed tabulation, bearing gonial as well as often two intergonal processes per suture. (Based on Deflandre & Cookson 1955, p. 264–265.)

Dimensions. Central body diameter 54–59 µm; process length 13–20 µm (Deflandre & Cookson 1955).

Biological affinity. Motile equivalent: *Gonyaulax spinifera* (Claparède & Lachmann 1859) Diesing 1866, according to Matsuoka et al. (1989, p. 94).

Intraspecific morphotypes. Following Limoges et al. (2018), morphotypes with short processes (<3 µm) should be informally called *Spiniferites hyperacanthus* – short-process morphotype, and specimens with three or more intergonal processes between pairs of gonial processes should be referred to as *Spiniferites hyperacanthus* – multi-intergonal morphotype.

Comparison. *Spiniferites lenzii* Below 1982 was described from the Albian (Lower Cretaceous) of Morocco; it has a central body length of 39–44 µm and a width of 38–43 µm, with processes of 8–15 µm long. LL expressed the opinion that *Spiniferites lenzii* should be considered a morphotype of *Spiniferites hyperacanthus* with higher septa. *Spiniferites lenzii* was also observed by Matsuoka (1983) from Upper Miocene to Lower to Middle Pleistocene of the Niigata district (central Japan). EM noted that Quaternary specimens of *Spiniferites lenzii* bear shorter processes than Below’s specimens. LL did not think the specimen depicted in Matsuoka (1983) belongs to this species because Matsuoka’s specimen shows low ridges rather than elevated septa. KNM stated in draft that Matsuoka (1983) described perforations at the base of the processes of his specimens of *Spiniferites lenzii*, which are not reported by Below (1982); Matsuoka’s specimens may correspond to *Spiniferites hyperacanthus* or another species. For comparison with *Spiniferites spinatus*, see Matsuoka (1983).

Remarks. During the first workshop, KNM repeated a remark already made by Rossignol (1964) that the antapical end is not visible on the published micrographs of the holotype of *Spiniferites hyperacanthus*, and therefore we cannot be certain that it has no antapical flange, without restudying the holotype. Otherwise participants thought this species is well understood. KZ considered it as a *Spiniferites mirabilis* with a reduced antapical flange. LL raised the question that if specimens have septa between processes, would they still belong to *Spiniferites hyperacanthus*? VP stated that the specimens from the continental slope off Nova Scotia depicted by Rochon et al. (1999, pl. 7, figs. 5–10) look different from *Spiniferites hyperacanthus* — these specimens only have one intergonal process per

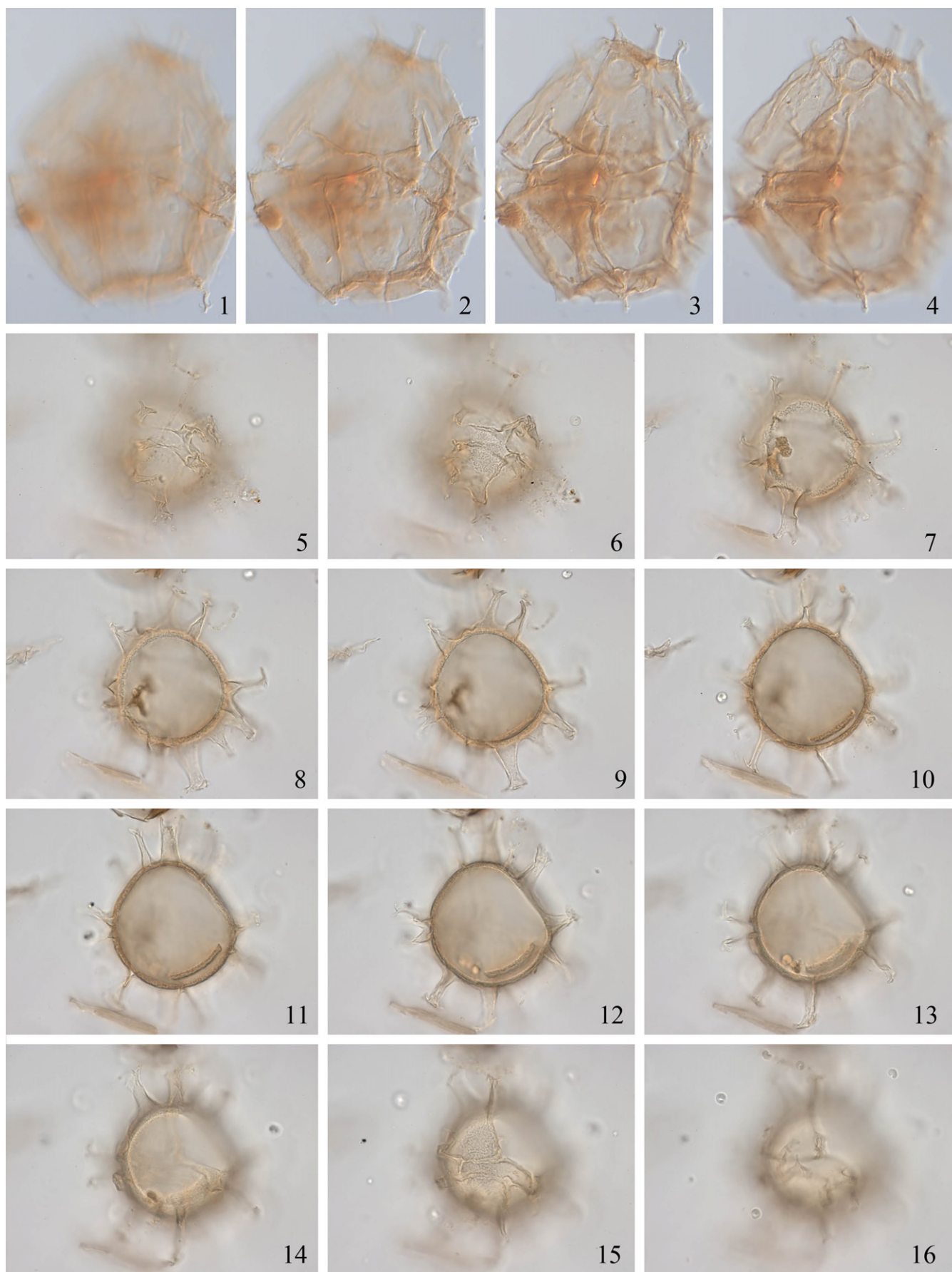


Plate 4. 1–4. Holotype of *Spiniferites hexatypicus* Matsuoka 1983 in dorsal view at high to low focus. Central body length 71 μm . Slide provided by KM, photographed by KNM. 5–16. Holotype of *Spiniferites ludhamensis* Head 1996 in left latero-ventral view at high to low focus. Central body length 41 μm . Slide provided by MJH, photographed by MJH.

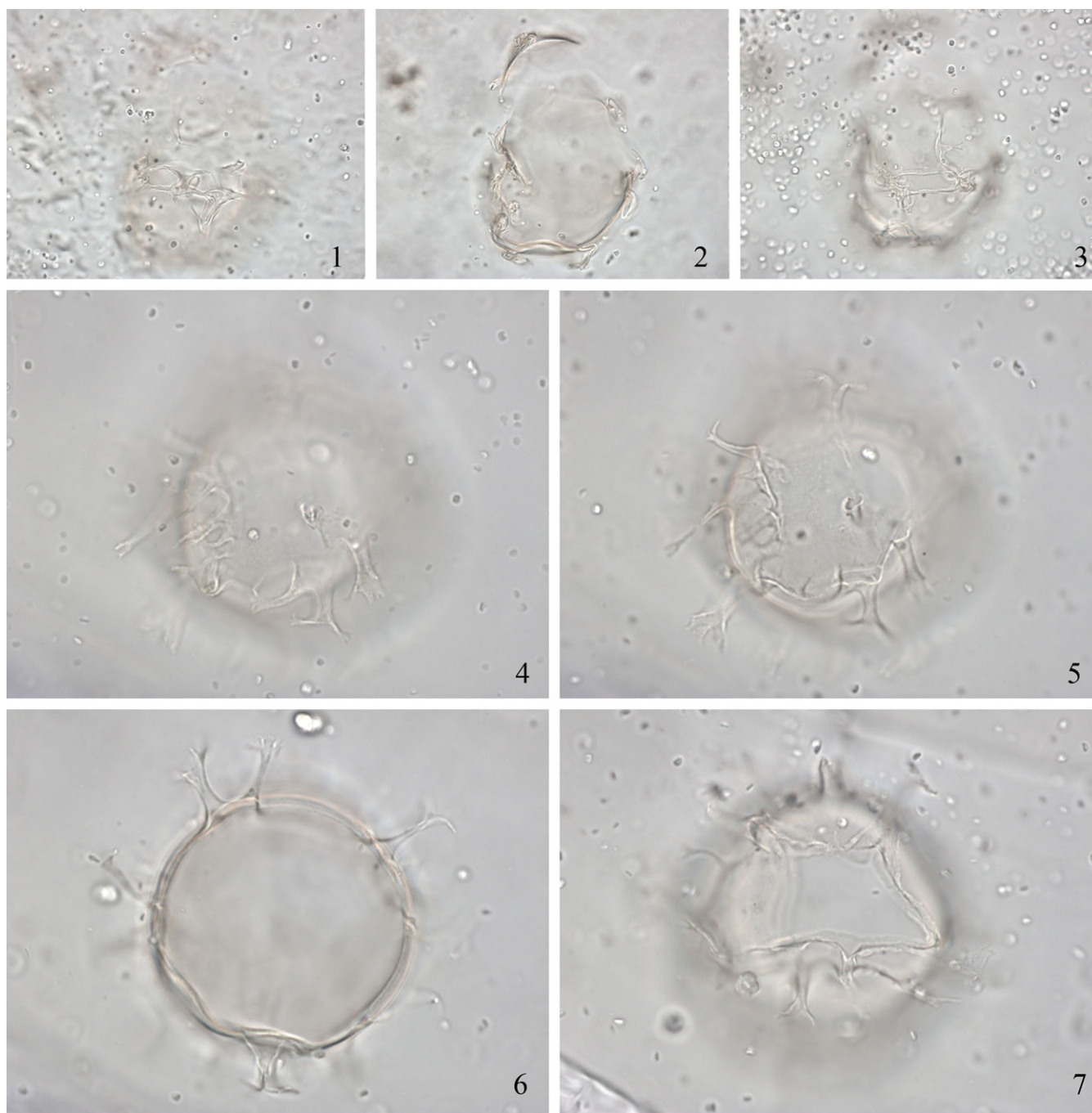


Plate 5. 1–3. Topotype of *Spiniferites nodosus* (Wall 1967) Sarjeant 1970 in lateral view, high to low focus. Present width of the central body = 46 μm . 4–7. Topotype of *Spiniferites pseudofurcatus* subsp. *obliquus* (Wall 1967) Lentin & Williams 1973 in ventral view at high to low focus. Central body length 45 μm , central body width = 44 μm . Slides provided by David Wall, photographed by MJH.

suture. This species is further discussed by Limoges et al. (2018) and Londeix et al. (2018).

2.20. *Spiniferites lazus* Reid 1974

Synonymy. None.

Holotype. Reid 1974, pl. 3, figs. 25–27.

Type locality. Pembroke, Wales, U.K.

Type stratum. Modern surface sediments (Reid 1974).

Etymology. From Old French, *laz* (lace), in reference to the fenestrate nature of the process bases (Reid 1974).

Distinguishing characters. Central body ovoid with a small apical boss. Wall thick with a microgranular to

microreticulate surface. Processes are exclusively gonal with wide fenestrate bases and connected by low sutural crests. Cingulum displaced by four times its width. The archeopyle is formed by loss of plate 3" and is reduced. The suture between 1 and 4 was not observed by Reid (1974), who indicated only three apical plates. (Based on Reid 1974, p. 604–605, and Rochon et al. 1999, p. 36.)

Dimensions. Central body length 44–58 μm , width 31–42 μm , thickness 31–39 μm ; wall thickness 1–1.5 μm ; cingulum width 5–8 μm ; process length 12–25 μm (Reid 1974).

Biological affinity. Unknown.

Intraspecific morphotypes. None.

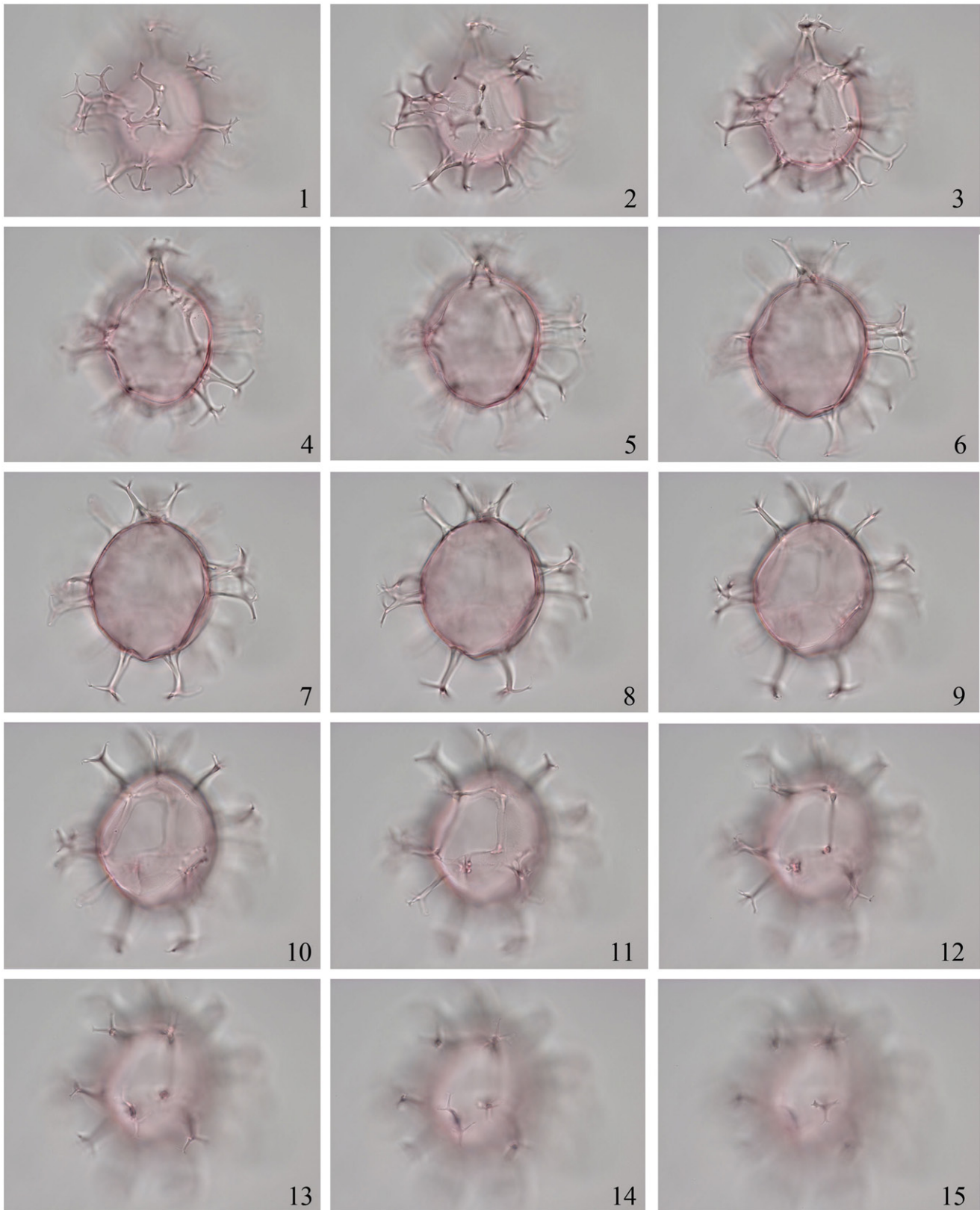


Plate 6. 1–15. Holotype of *Spiniferites rhizophorus* Head in Head & Westphal 1999 in ventral view at high to low focus. Central body length 50 μm . Slide provided by MJH, photographed by MJH.

Comparison. This species differs from all other *Spiniferites* on the basis of its ovoid shape, apical boss, and fenestrate process bases. *Spiniferites bentorii* has a pear-shaped central body. *Spiniferites septentrionalis* has large fenestrations in the

distal ends of its processes. *Spiniferites hainanensis* has intergonal processes (Sun Xuekun & Song Zhichen 1992).

Remarks. Reid (1974) mentioned the occurrence of occasional intergonal processes in the original description, but

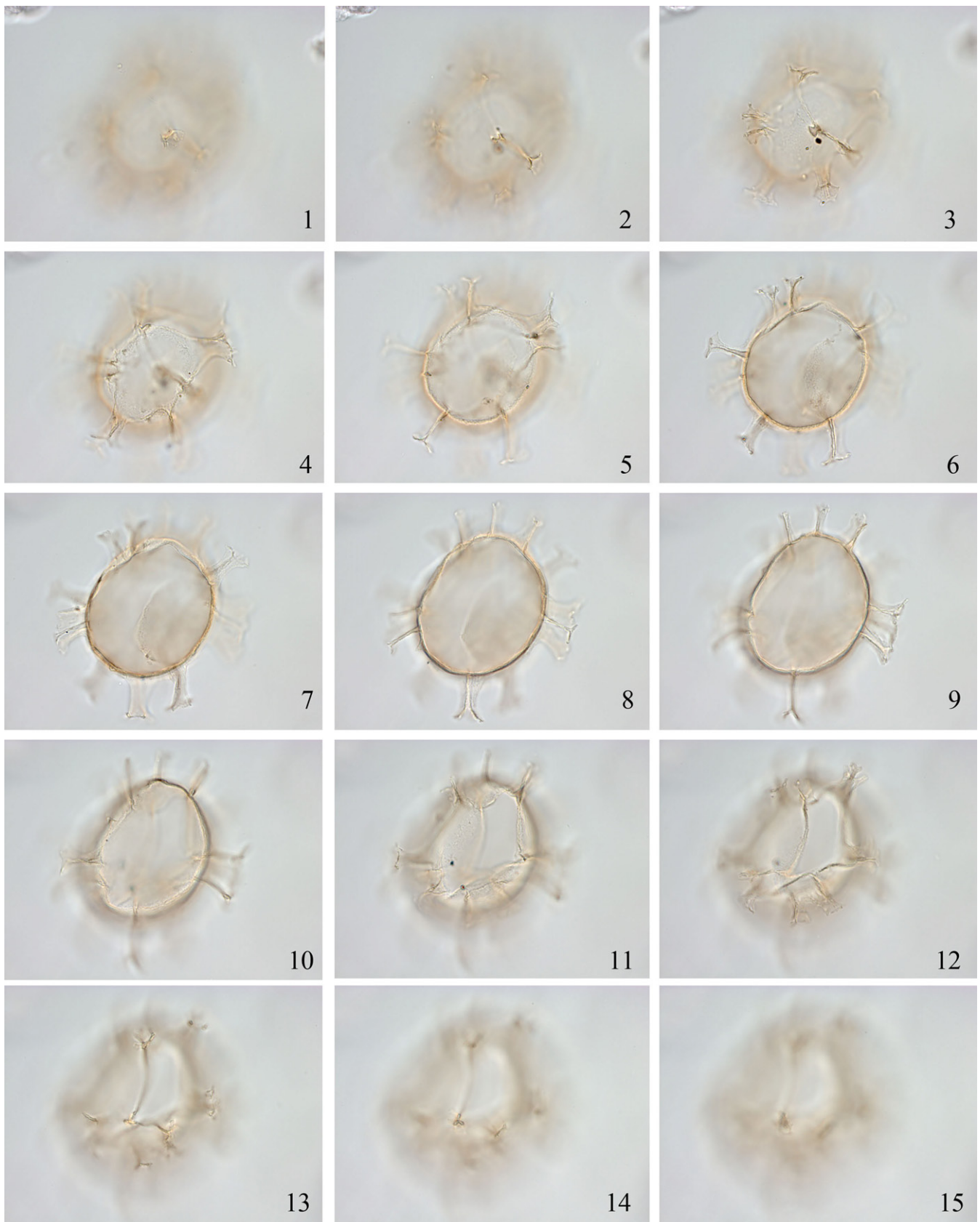


Plate 7. 1–15. Holotype of *Spiniferites ristingensis* Head 2007 in ventral view at high to low focus. Central body length 42 µm. Slide provided by MJH, photographed by MJH.

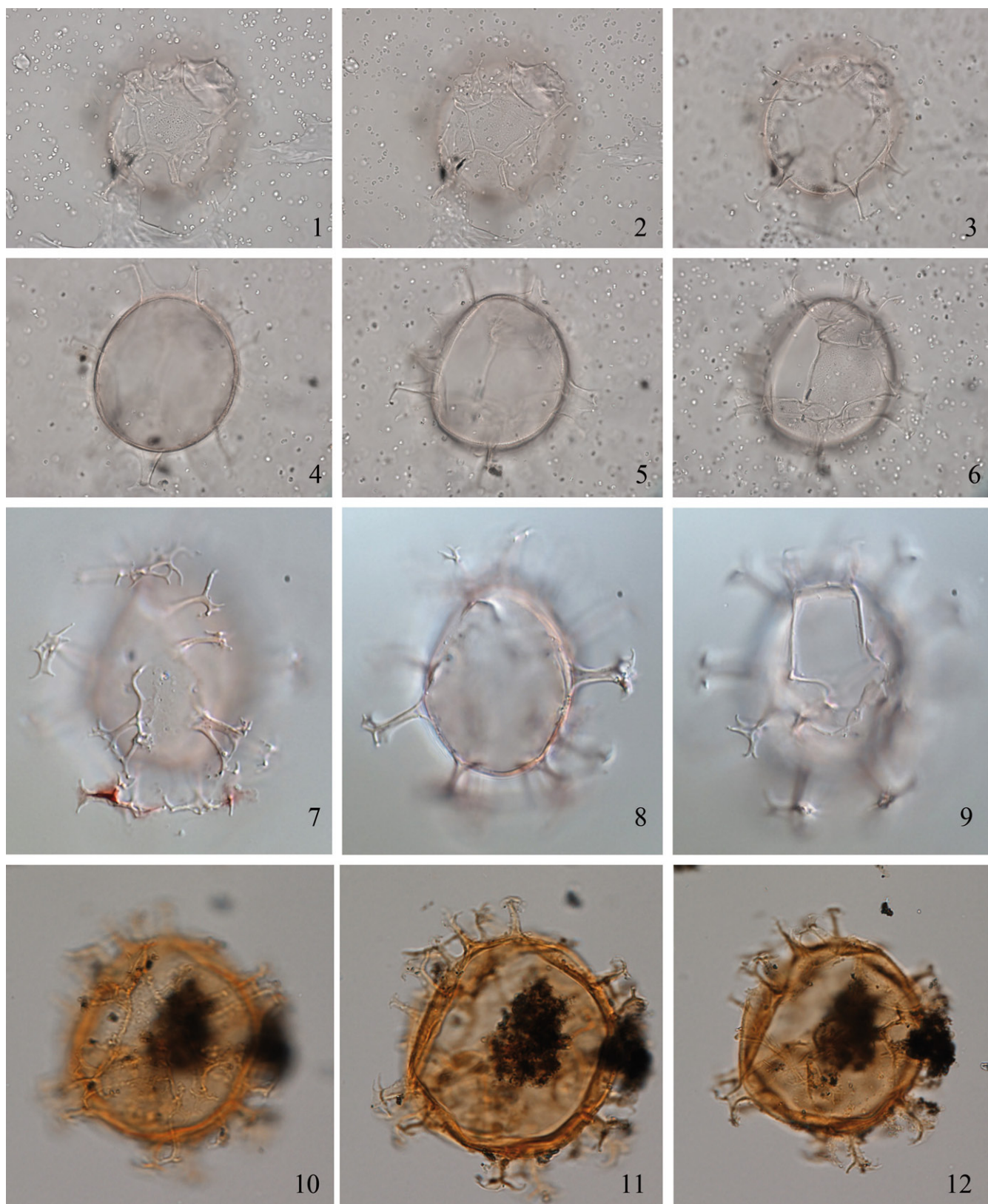


Plate 8. 1–6. *Spiniferites scabratus* (Wall 1967) Sarjeant 1970 in right lateral view at high to low focus. Central body length = 56 μm , central body thickness = 49 μm . Slide provided by David Wall, photographed by MJH. 7–9. Holotype of *Spiniferites septentrionalis* Harland 1979 in ventral view at high to low focus. Central body length 35 μm . Photographed by James B. Riding. 10–12. Holotype of *Spiniferites strictus* Matsuoka 1983 in ventral view at high to low focus. Central body length 67 μm . Slide provided by KM, photographed by KNM.

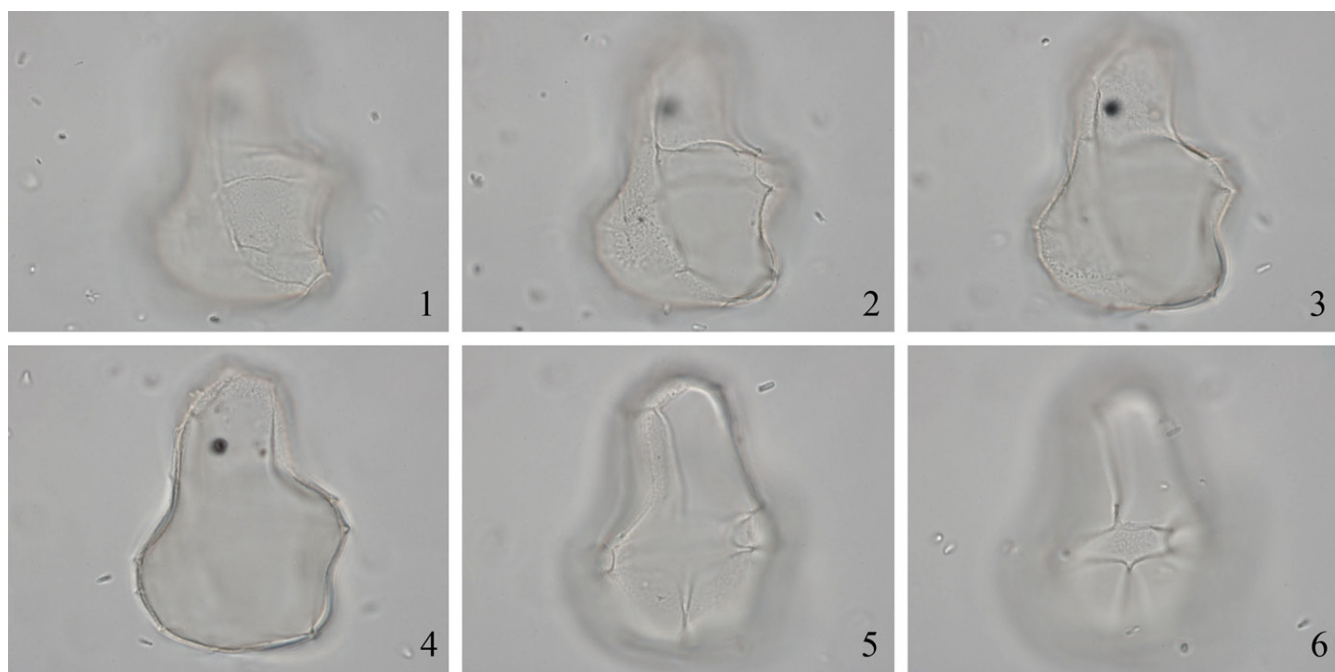


Plate 9. 1–6. *Impagidinium inaequalis* (Wall and Dale in Wall et al. 1973) Londeix et al. 2009 in. left lateral view, at high to low focus, central body length = 54 μm . Slide provided by David Wall, photographed by MJH.

this feature has not been observed by anyone attending the workshops. The species is discussed by Gurdebeke et al. (2018).

2.21. *Spiniferites ludhamensis* head 1996 (Plate 4, figures 5–16)

Synonymy. None.

Holotype. Head 1996b, fig. 12, nos. 5–9.

Type locality. Royal Society borehole, Ludham, Norfolk, England, U.K.

Type stratum. Antian regional pollen zone; Gelasian, Lower Pleistocene (Wall & Dale 1968, Head 1996b).

Etymology. Named after the type locality (Head 1996b).

Distinguishing characters. This species is characterised by a central body wall with a thin pedium, and thicker luxuria consisting of a thin tectum supported by funnel-shaped invaginations, solid at the base where they meet the pedium. The central body is ovoid and has no apical protuberance. The processes are gonal and occasionally intergonal, multifurcate and bifurcate (possibly with second-order branching), hollow along their length, arising from low hollow sutural crests. The sutural crests lack the funnel-shaped invaginations. The apex is indicated by a tapering spine-like hollow process with smaller side branches. The archeopyle is formed by loss of plate 3", principal archeopyle suture closely follows plate boundaries and hence has well-defined angles. (Based on Head 1996b, p. 557.)

Dimensions. Central body length 38 (42.2) 49 μm , equatorial diameter 34 (37.3) 41; wall thickness ~ 1.1 (1.5) 1.8 μm ; average process length 10 (12.9) 15 μm (Head 1996b).

Biological affinity. Unknown.

Intraspecific morphotypes. None.

Comparison. This species is distinguished by its unusual wall structure with numerous invaginations, thin-walled hollow processes whose branched distal terminations are also hollow and may form small tubules, and sutural folds rather than the solid crests which are more typical for the genus (Head 1996b).

Remarks. During the first workshop, EM wondered whether there is only one layer with vesicles in *Spiniferites ludhamensis*. MJH replied that this is the case. EM then stated that *Hafniasphaera* has several layers and wondered whether this characteristic should be used to distinguish *Spiniferites* and *Hafniasphaera*, and if the description of the genus *Spiniferites* therefore should be emended. KNM noted in draft that the original description of *Hafniasphaera* describes the wall structure as "composed of two layers, endophragm and periphragm. One or both of these layers contain numerous evenly distributed vesicles (vacuoles). The vesicles are spheroidal or, if interconnected, they may form a fine reticulum internal in the cyst wall" (Hansen 1977). This species is further discussed by Limoges et al. (2018).

2.22. *Spiniferites membranaceus* (Rossignol 1964) Sarjeant 1970

Synonymy. *Hystrichosphaera furcata* var. *membranacea* Rossignol 1964, p. 86, pl. 1, figs. 4, 9–10; pl. 3, figs. 7, 12.

Hystrichosphaera ramosa var. *membranacea* (Rossignol 1964) Davey & Williams 1966, p. 37.

Hystrichosphaera membranacea (Rossignol 1964) Wall 1967, p. 102.

Holotype. Rossignol 1964, pl. 1, figs. 4, 9–10.

Type locality. Ashkelon borehole St. 39D, coastal plain, Israel.

Type stratum. Pleistocene or Holocene sediments (Rossignol 1964).

Etymology. Not specified by Rossignol (1964), but presumably in reference to the distinct membranous flange in the antapical region that characterises this species.

Distinguishing characters. Central body ovoid with no apical boss. Surface of the outer wall is microgranulate to microrugulate. Processes are exclusively gonial, and are distally furcate with recurved bifurcate tips. Sutural crests are mostly low but are high at the antapex where they form a conspicuous membrane between antapical processes. The cingulum is inclined and displaced by twice its width, and the sulcus is slightly sigmoid and moderately wide. Tabulation is typical for the genus, and sulcal plates are visible. The archeopyle is formed by loss of plate 3". (Based on Rossignol 1964, p. 86, Reid 1974, p. 605–606, Lewis et al. 1999, p. 115–117, Rochon et al. 1999, p. 36–38, Ellegaard et al. 2003, p. 154–156.)

Dimensions. Central body length 57 µm, width 50 µm; process length 20–25 µm (Rossignol 1964). Central body length 34–44 µm, width 34–43 µm; cingulum width 5–8 µm; length of antapical flange 2–21 µm, process length 12–17 µm (Reid 1974).

Biological affinity. Previously *Gonyaulax spinifera* (Claparède & Lachmann 1859) Diesing 1866 according to Dale (1976, table 2, p. 45) and Dodge (1989, p. 289). Ellegaard et al. (2003) found the motile stage of *Spiniferites membranaceus* to represent an undescribed species of *Gonyaulax*, and using a unified approach to cyst and motile stage taxonomy/nomenclature, transferred *Spiniferites membranaceus* to the genus *Gonyaulax*, as *G. membranacea* (Rossignol 1964) Ellegaard et al. 2003. However, we follow the prevailing practice among cyst researchers of using dual taxonomy/nomenclature (Head et al. 2016; but see Ellegaard et al. 2018), and hence the name *Spiniferites membranaceus* is here retained.

Intraspecific morphotypes. LL remarked during the workshop that specimens with an antapical flange such as those depicted by Wall (1967, pl. 14, figs. 14–15) from the Caribbean should be referred to as *Spiniferites* cf. *membranaceus* because overall the processes are relatively short and the antapical flange is supported by distinctly stout and rod-like processes unlike those of the holotype and specimens mentioned above as typical.

Comparison. *Spiniferites membranaceus* is distinguished from *Spiniferites mirabilis* by its absence of intergonal processes. See Londeix et al. (2018) for an extended comparison with other similar species.

Remarks. Wall et al. (1977) (repeated by Harland 1983) stated that *Spiniferites membranaceus* sensu Reid (1974) is probably not conspecific with that of Rossignol (1964). To verify this, KNM proposed that Rossignol's holotype should be restudied, but EM replied that it is probably lost. MJH suggested that the topotype material be restudied. Rochon et al. (1999) noted the presence of occasional intergonal processes, but this could not be confirmed by workshop participants. This species is further discussed by Gurdebeke et al. (2018).

2.23. *Spiniferites mirabilis* (Rossignol 1964) Sarjeant 1970

Synonymy. *Hystrichosphaera mirabilis* Rossignol 1964 p. 86–87, pl. 2, figs. 1–3; pl. 3, figs. 4–5. [The name was invalid in Rossignol (1962, p. 132) because no illustration was provided and no holotype designated.]

Spiniferites splendidus Harland 1979, p. 537, pl. 3, figs. 1–2.

Holotype. Rossignol 1964, pl. 2, figs. 1–2.

Type locality. Ashdod Yam borehole, coastal plain, Israel.

Type stratum. Pleistocene or Holocene (Rossignol 1964).

Etymology. From the Latin *mirabilis*, meaning admirable (Rossignol 1964).

Distinguishing characters. Central body ovoid with a smooth to granular surface. The processes are gonial as well as intergonal, slender, and connected by generally low to barely discernible crests. However, a prominent antapical flange connects the two antapical processes. The sulcus is slightly oblique and the cingulum is displaced by two times its width. The archeopyle is formed by the loss of plate 3" and is reduced. (Based on Rossignol 1964, p. 86–87, and new observations by AL, LL and KNM.)

Dimensions. Central body length 40–70 µm, width 35–60 µm; process length 15–22 µm (Rossignol 1964).

Biological affinity. Related to *Gonyaulax spinifera* according to cyst-theca experiments by Wall & Dale (1967, p. 352) and Wall & Dale (1968, p. 270); reproduced by Dale (1983) and Dodge (1985, p. 215; 1989, p. 289). Sonneman & Hill (1997) and Morquecho et al. (2009) also conducted cyst-theca experiments on *Spiniferites mirabilis* and also identified the motile stage as *Gonyaulax spinifera*.

Intraspecific morphotypes. *Spiniferites mirabilis* subsp. *serratus* Limoges et al. (2018), originally described by Matsuoka (1983) from the Pliocene (or younger) Nishiyama Formation, Ishiji, Nishiyama-cho, Niigata prefecture (central Japan). The central body length is 45–54 µm, width 47–50 µm, with process length 7–9 µm. It differs from *Spiniferites mirabilis* subsp. *mirabilis* (autonym) in having "many short conical to subconical intergonal processes" (Matsuoka 1983). Limoges et al. (2018) consider specimens with three or more intergonals as belonging to *Spiniferites mirabilis* subsp. *serratus*.

Comparison. The main distinction between this species and *Spiniferites hyperacanthus* is the presence of an antapical flange. The main distinction between *Spiniferites mirabilis* and *Spiniferites membranaceus* is the presence of intergonal processes in *Spiniferites mirabilis*.

Remarks. *Spiniferites splendidus* was described from the Upper Miocene–Lower Pliocene of DSDP Hole 400 A (Bay of Biscay) by Harland (1979). According to Harland (1979), *Spiniferites splendidus* is larger than *Spiniferites mirabilis* and has many membranous processes. However, during the workshop MJH remarked that Harland (1979) did not provide measurements of *Spiniferites mirabilis* but that his illustrated specimens are not markedly different in size from the single specimen of *Spiniferites splendidus* illustrated by Harland (1979). During the round table discussion, LL stated that there are fewer processes on *Spiniferites splendidus* than on *Spiniferites mirabilis*. MJH replied that Harland (1979) did not

describe the number of processes as diagnostic, so maybe he just illustrated an aberrant specimen. SD remarked that there seem to be membraneous processes on the sulcus, something not seen in *Spiniferites mirabilis*. MJH expressed some concern about the fact that only two specimens were illustrated by Harland (1979) and noted a further need to study topotype material. The holotype was rephotographed by James B. Riding and the synonymy is further discussed by Limoges et al. and Londeix et al. (2018).

LL remarked during the first workshop that it is necessary to add to the original description that processes are hollow and can be distally open, as is the antapical flange. He added that he has, however, only seen this in Miocene specimens; AR stated during draft that he has made similar observations in specimens from Argentina. VP added that it is remarkable that *Spiniferites mirabilis* and *Spiniferites membranaceus* were described from the same sample. LL added after the first workshop that several modern Mediterranean specimens have hollow and open processes. KNM also added that it is remarkable that this species can have very faint to no sutures, which could place it in *Achomosphaera*. The species is further discussed by Limoges et al. (2018) and Londeix et al. (2018).

2.24. *Spiniferites multisphaerus* Price & Pospelova 2014

Synonymy. None.

Holotype. Price & Pospelova 2014, pl. 1, figs. 1–13.

Type locality. Core MD02–2515, Guaymas Basin, Gulf of California, Mexico.

Type stratum. Upper Quaternary sediments (Price & Pospelova 2014).

Etymology. From the Latin *multi* (many) and *sphaerae* (spheres), in reference to the characteristic central body wall structure that features multiple vacuoles (Price & Pospelova 2014).

Distinguishing characters. Ovoid to pear-shaped central body with a pronounced apical protuberance. Wall is relatively thick and contains a single layer of vacuoles. Processes are stubby, furcate and also contain vacuoles. Tabulation is clearly expressed and is typical of the genus. The archeopyle is formed by loss of plate 3". (Based on Price & Pospelova 2014, p. 7–13.)

Dimensions. Central body length (including apical protuberance) 42.6 (52.4) 66.5 µm; wall thickness 1.0 (1.5) 2.1 µm; mean length of processes 1.5 (4.4) 8.0 µm (Price & Pospelova 2014).

Biological affinity. Unknown.

Intraspecific morphotypes. None.

Comparison. *Spiniferites multisphaerus* is distinguished by the presence of vacuoles in the cyst wall, processes and sutural septa; this feature is not known in other Quaternary *Spiniferites* species. In terms of extant taxa, *Spiniferites multisphaerus* most closely resembles *Spiniferites bentorii*, as both have a pronounced apical boss and 'shoulders' on the epicyst. It is distinguished from *Spiniferites bentorii* by the presence of the vacuoles. In addition, the surface of *Spiniferites*

multisphaerus appears reticulate whereas *Spiniferites bentorii* appears smooth to microgranular (Price & Pospelova 2014). *Spiniferites multisphaerus* differs from *Spiniferites ludhamensis* in that the latter has a wall-structure comparable to bubble-wrap.

Remarks. During the first round table discussion, there was the general question, put forward by EM, as to whether this species should be transferred to *Hafniasphaera*, a genus described by Hansen (1977) that is distinguished from *Spiniferites* by the presence of one or two layers containing spheroidal vacuoles or vacuoles forming a fine reticulum inside the cyst wall. Since *Spiniferites multisphaerus* contains a single layer of vacuoles (as pointed out by AP), it could be assigned to *Hafniasphaera*. VP expressed concern that it is difficult to draw the line with other, increasingly more granulated walls. EM pointed out that if we accept a vacuolated wall for *Spiniferites*, the genus description of Sarjeant (1970) has to be emended. This species is further discussed by Limoges et al. (2018). Londeix et al. (2018) transferred this species to *Hafniasphaera*.

2.25. *Spiniferites nanus* Matsuoka 1976

Synonymy. non *Spiniferites bulloideus* (Deflandre & Cookson 1955) Sarjeant 1970.

Holotype. Matsuoka 1976, pl. 28, figs. 1–3.

Type locality. Nara City, Japan.

Type stratum. Utahime Member, Saho Formation; Lower Pleistocene (Matsuoka 1976).

Etymology. Not specified by Matsuoka (1976), but is from the Latin *nanus*, for dwarf, in reference to the short process length (confirmed by KM). The epithet is a noun in apposition.

Distinguishing characters. The central body has a rounded conical epicyst and a rounded hypocyst. The outer wall is smooth or very finely granular. The sulcal region is almost straight and widens posteriorly. The relatively broad cingulum is displaced by one to two times its own width. The short processes with bifurcate, trifurcate or acuminate tips are mostly gonial, with intergonial processes occurring occasionally. The short acuminate processes with wide bases are formed from membraneous sutures. The tabulation is typical for the genus, and the small triangular plate 6" is extended longitudinally. The archeopyle is formed by loss of plate 3" and is reduced. (Based on Matsuoka 1976, p. 111.)

Dimensions. Central body length 41–55 µm, width 35–54 µm; process length 5–11 µm (Matsuoka 1976, p. 111).

Biological affinity. Unknown.

Intraspecific morphotypes. None.

Comparison. Matsuoka (1976) remarked that *Spiniferites bulloideus* differs from *Spiniferites nanus* in having a relatively larger central body (length 54–64 µm, width 30–37 µm) and longer and exclusively gonial processes (10–15 µm); measurements taken from Deflandre & Cookson (1955).

Remarks. KM stated in a communication to KNM in draft that "I now believe this species is a junior synonym of the relatively broad species concept of *Spiniferites bulloideus*. *Spiniferites nanus* is a short-process form of *Spiniferites*

bulloideus, which presumably exhibits similar morphological variability in processes as documented for cysts of *Protoceratium reticulatum* and cysts of *Lingulodinium polyedra*." However, according to the original description, *Spiniferites nanus* can sometimes have intergonal processes. Thus, *Spiniferites nanus* may not be synonymous with *Spiniferites bulloideus*, but we recommended that the former species be restricted to the holotype. Matsuoka (1987b) also observed specimens from the Holocene close to Kawasaki city (Japan). See also Limoges et al. (2018).

2.26. *Spiniferites nodosus* (Wall 1967) Sarjeant 1970 (Plate 5, figures 1–3)

Synonymy. *Hystrichosphaera nodosa* Wall 1967, p. 101, pl. 14, figs. 7–9; text-fig. 2. non *Spiniferites* [as *Hystrichosphaera*] *bentorii*, according to Reid (1974, p. 598); we follow Lentin & Williams (1981, p. 264) in retaining *Spiniferites nodosus*.

Holotype. Wall, 1967, pl. 14, figs. 7–9.

Type locality. Core A240/18, Cariaco Trench, off Venezuela.

Type stratum. Quaternary (Wall 1967).

Etymology. Not specified by Wall (1967), but probably from the Latin *nodosus*, meaning knotty, in reference to the shape of the processes.

Distinguishing characters. Ovoid central body with weakly truncated apices. The plate areas are defined by distinct but low ($\leq 1\mu\text{m}$) sutural septa and are typical in number and arrangement for the genus. The characteristic processes are exclusively gonial, small, either bifurcate or trifurcate and recurve strongly towards their own bases or lie along the cyst surface so that there appears to be a small pad of tissue at each junction. Only rarely do the processes project more than a few microns above the test wall. The archeopyle is formed by loss of plate 3" and has a weakly inclined cingulum. (Based on Wall 1967, p. 101–102.)

Dimensions. Central body length 31–62 μm , width 28–52 μm (Wall 1967).

Biological affinity. Related to *Gonyaulax digitale*, according to Wall & Dale (1967, p. 352), repeated in Wall & Dale (1968, p. 269).

Intraspecific morphotypes. None.

Comparison. PJM remarked that this species is difficult to distinguish from *Spiniferites bentorii*; indeed, Reid (1974) had proposed that *Spiniferites nodosus* is a junior synonym of *Spiniferites bentorii*. However, LL is not convinced that the holotype of *Spiniferites nodosus* falls within the range of *Spiniferites bentorii* because its central body lacks the typical pear-shape and is smaller (31–62 μm in length, 28–52 μm in width). Therefore, we recommend restricting this name to the holotype.

Remarks. MJH noted during the first workshop that it was unclear whether one or two specimens were assigned as the holotype, and thus questioned whether the species name is valid. However, in draft, a personal communication of KNM with David Wall confirmed that it is a single specimen that was rotated into different views. Wall (1967, p. 102) remarked that "This species gives the impression

that as a cyst it was closely pressed against its parental thecal covering and that the spines were unable to develop fully, but it is not necessarily an immature form". However, participants agreed that the "strongly recurved processes" of *Spiniferites nodosus* are probably due to preservation. MJH in draft provided the following information: "The holotype is preserved on a single grain mount and is broken and somewhat compressed. The central body has an apical protrusion of about 1.0 μm , and a wall thickness of about 0.3 μm . The surface is very faintly and finely granulate (scabrate). Sutural septa are about 1.5 μm high. There is a slight separation of wall layers at the base of septa. Processes are mostly gonial, although one intergonal process was clearly identified. Gonial process are strongly shortened by crumpling, making it impossible to determine their exact morphology. I agree that the name is best restricted to the holotype."

2.27. *Spiniferites pachydermus* (Rossignol 1964) Reid 1974

Synonymy. *Hystrichosphaera furcata* var. *pachyderma* Rossignol 1964, p. 86, pl. 1, figs. 1–2; pl. 3, fig. 6.

"*Hystrichosphaera ramosa* var. *pachyderma*" Harland & Downie 1969, p. 232.

Spiniferites ramosus subsp. *pachydermus* (Rossignol 1964) Lentin & Williams 1973, p. 130.

Holotype. Rossignol 1964, pl. 1, figs. 1–2.

Type locality. Ashdod borehole 15/0, coastal plain, Israel.

Type stratum. Pleistocene or Holocene (Rossignol 1964).

Etymology. Derived from the Greek, *pachy*, thick, and *derma*, skin (Head 1996a, p. 1232), in reference to the thick cyst wall.

Distinguishing characters. Central body ovoid with a low apical boss. The wall is thick ($>1\mu\text{m}$) with a microreticulate/perforate surface. The processes are stout and exclusively gonial, and joined by mostly low sutural septae that express the tabulation. Notable exceptions to these low crest heights can be found between the two processes between the anterior sulcal plate and the apical plates 1' and 4', which are always connected by a crest that reaches the distal ends of the processes, and the elevated crest heights for closely spaced processes along the cingulum, particularly for the processes contacting on the left of 1c and 2'''. The processes are variable in length, becoming progressively shorter from the antapex to the apex. The processes are formed at the convergence of three sutures. Distally the processes are petaloid and trifurcate with slender recurved bifid tips. Often claustra are present at the base of the processes or on the connecting crests. Specimens with processes that appear broken off were also encountered. Tabulation is typical for the genus. The antapical plate is asymmetrical. The cingulum is sinistral and displaced by a distance 3.5 times its width. The sulcus is moderately wide and almost straight, and all sulcal plates are visible. The archeopyle is formed by loss of plate 3", is reduced, and has a serrated margin. The operculum is free. (Based on Mertens et al. 2015, p. 563–566.)

Dimensions. Central body length 61 μm , width 52 μm , wall thickness 3 μm (Rossignol 1964). Central body length 33–54 μm , width 37–44 μm ; cingulum width 5–9 μm ; maximum process length 19 μm (Reid 1974). Central body length (including low apical boss) 36.6 (42.6) 48.1 μm , width (measured along the cingulum) 30.6 (35.7) 41.0 μm ; average length of six processes per cyst 5.3 (10.2) 17.7 μm (Mertens et al. 2015).

Biological affinity. *Gonyaulax ellegaardiae* Mertens, Aydin, Takano, Yamaguchi & Matsuoka 2015, according to Mertens et al. (2015).

Intraspecific morphotypes. None.

Comparison. The microreticulate/perforate wall distinguishes *Spiniferites pachydermus* from all other described species of *Spiniferites* (Mertens et al. 2015).

Remarks. The consensus during the first workshop was that a restudy of the holotype was needed, but subsequent efforts by EM to locate the holotype at the Muséum National d'Histoire Naturelle in Paris have not been successful. LL identifies *Spiniferites pachydermus* through its thick wall and somewhat larger size than other species. However, KZ replied that Mediterranean species are always larger than elsewhere, and that this might complicate identification; FS agreed. LL remarked that in the specimen illustrated by Rossignol (1964, fig. 6) the wall is very thick, and thus she compared it with *Achomosphaera crassipellis* (wall thickness 1.5–2 μm ; Deflandre & Cookson 1955, p. 265); but generally the wall of *Spiniferites pachydermus* is not that thick.

"*Hystrichosphaera ramosa* var. *pachyderma*" as proposed by Harland & Downie (1969) is an invalid combination since the basionym was not fully referenced.

2.28. *Spiniferites pacificus* Zhao Yunyun & Morzadec-Kerfourn 1994

Synonymy. non *Spiniferites* cf. *delicatus* of Matsuoka 1992, pl. 1, fig. 4.

Holotype. Zhao Yunyun & Morzadec-Kerfourn 1994, pl. 1, figs. 1a–c.

Type locality. ODP Leg 126, Site 791, Izu–Bonin region, western North Pacific.

Type stratum. Lower or Upper Pleistocene (Zhao Yunyun & Morzadec-Kerfourn 1994).

Etymology. Derived from its presence in the Pacific Ocean (Zhao Yunyun & Morzadec-Kerfourn 1994).

Distinguishing characters. Central body spheroidal to ovoid with a microgranular surface, and bearing both gonol and intergonal processes (one between each of a pair of gonol processes). The two large, hollow antapical processes are longer and membranous and open distally. The tabulation is typical for the genus: 3'–4', 0a, 6', 6c, 5–6', 1p, 1'. The archeopyle is formed by loss of plate 3". (Based on Zhao Yunyun & Morzadec-Kerfourn 1994, p. 268–269.)

Dimensions. Central body length 25.6–35.3 μm , width 28.8–29.9 μm ; average length of gonol processes 10.8 μm , average length of antapical processes 13.2 μm (Zhao Yunyun & Morzadec-Kerfourn 1994).

Biological affinity. Unknown.

Intraspecific morphotypes. None.

Comparison. This species differs from other species that have two pronounced antapical processes (*Spiniferites falcipedi*, *Spiniferites firmus* and *Spiniferites bulloideus* sensu Wall 1965) by the presence of intergonal processes.

Remarks. *Spiniferites* cf. *delicatus* of Matsuoka (1992) does not have intergonal processes, as here confirmed by KM, and thus is not conspecific with *Spiniferites pacificus*.

KNM remarked during the first workshop that it was not clear whether the specimens illustrated through light micrographs (Zhao Yunyun & Morzadec-Kerfourn 1994, pl. 1, figs. 1–3) show intergonal processes, although specimens illustrated through SEM micrographs (Zhao Yunyun & Morzadec-Kerfourn 1994, pl. 2, figs. 1–3) clearly bear intergonal processes. LL mentioned in draft that the sutural features of this species are so faint that it could be considered as belonging to *Achomosphaera*.

2.29. *Spiniferites pseudofurcatus* subsp. *obliquus* (Wall 1967) Lentin & Williams 1973 (Plate 5, figures 4–7)

Synonymy. *Hystrichosphaera tertiaria* var. *obliqua* Wall, 1967, p. 103, pl. 14, fig. 16; text-fig. 2.

Holotype. Wall 1967, pl. 14, fig. 16.

Type locality. Core A254/327, Yucatan Basin, Caribbean Sea.

Type stratum. Upper Pleistocene–Holocene; 400 cm depth (Wall 1967).

Etymology. Not specified by Wall (1967), but the subspecific epithet presumably derives from the oblique nature of the longitudinal sulcus.

Distinguishing characters. The central body is ovoid, sometimes with a low apical protuberance, and has a smooth to weakly granular surface. The processes are distinctive, gonol trifurcate with secondary branches that tend to be parallel and often are connected by delicate membranes; occasional intergonal processes are present. Two dorsal antapical processes are prominent. The tabulation is typical for the genus. The sulcus is oblique, narrows anteriorly and widens posteriorly; the cingulum is strongly displaced at its ends. (Based on Wall 1967, p. 103.)

Dimensions. Central body length 40–50 μm ; process length 10–12 μm (Wall 1967).

Biological affinity. Unknown.

Intraspecific morphotypes. None.

Comparison. According to Wall (1967), *Spiniferites pseudofurcatus* subsp. *obliquus* (as *Hystrichosphaera tertiaria* var. *obliqua*) is a small morphotype of *Hystrichosphaera tertiaria* Eisenack & Gocht 1960. The latter was first described by Eisenack (1954, as "*Hystrichosphaera* cf. *furcata*") from the Oligocene, with a central body length of 50–70 μm , and total diameter of 80–133 μm . *Hystrichosphaera tertiaria* is now considered a synonym of *Spiniferites pseudofurcatus* (Klumpp 1953) Sarjeant 1970 (Gocht 1969; Sarjeant 1970), the type of which is from the Upper Eocene of Germany. *Spiniferites bentorii* has a more prominent apical protuberance (Wall 1967).

Remarks. Wrenn & Kokinos (1986, pl. 7, fig. 1–2) also depicted this subspecies from the Lower to Upper Pliocene of the Gulf of Mexico (image reproduced in de Vernal & Mudie 1992, pl. 4, fig. 3). During the first workshop, MJH noted that he has seen the holotype and that it does not look particularly distinctive - he would just call it *Spiniferites* sp. KZ suggested that the subspecies should be restricted to the holotype. LL stated that the assemblages studied by Wrenn & Kokinos (1986) included many reworked specimens, so he questions the status of the type material of this taxon.

2.30. *Spiniferites ramosus sensu Rochon et al. (1999)*

Synonymy. *Spiniferites bulloideus* (auct. non Deflandre & Cookson) Sarjeant; Reid 1974, pl. 2, figs. 17–19.

Spiniferites ramosus (auct. non Ehrenberg) Mantell; Harland 1977, pl. 1, figs. 5–6.

Spiniferites ramosus (auct. non Ehrenberg) Mantell *sensu lato*; Rochon et al. 1999, pl. 9, figs. 4–6.

non *Spiniferites ramosus* var. *ramosus* (Ehrenberg) Mantell; Davey & Rogers 1975, pl. 1, fig. 5.

Holotype. Not relevant.

Type locality. Not relevant.

Type stratum. Not relevant.

Etymology. Not relevant.

Distinguishing characters. Central body ovoid to spheroidal with or without apical boss, and a smooth pedium and tegillum. Processes are exclusively gonol, long, hollow, and have long distal furcations with bifurcate tips. Sutural crests are low but rise towards the gonol processes to which they connect. Narrow, thread-like pairs of trabeculae between adjacent process tips are sometimes developed. Tabulation is typical for the genus, with plates 1' and 4' appearing to be fused on the cysts. The cingulum is displaced by its own width and the archeopyle is formed by loss of plate 3". (Based on Reid 1974, p. 600–601; as *Spiniferites ramosus* in Harland 1977, p. 102–103; and as *Spiniferites ramosus sensu lato* in Rochon et al. 1999, p. 38.)

Dimensions. Central body length 30–46 µm (Rochon et al. 1999) and 41–46 µm (Reid 1974), width 19–27 µm; cingulum width 6–8 µm; maximum process length 8–16 µm (Reid 1974).

Biological affinity. Through incubation experiments on material from Harrington Sound (Bermuda), Wall & Dale (1970) related *Spiniferites ramosus* to *Gonyaulax spinifera*; however, their specimens bear both gonol and occasional intergonol processes. They later called it the "Bermuda type" or "*Spiniferites ramosus sensu Wall & Dale 1970*" (Wall et al. 1977). The lack of detail in the description, particularly of the cyst wall, does not exclude the possibility that this is a different taxon from *Spiniferites ramosus sensu lato* of Rochon et al. (1999). Much later, Lewis et al. (1999) related *Spiniferites ramosus* to *Gonyaulax spinifera*, with the morphology of the cyst similar to the morphological concept described above. Cysts attributed to *Spiniferites ramosus* formed in culture experiments and related to *Gonyaulax spinifera* by Rochon et al. (2009) correspond relatively well to the description of Rochon et al. (1999), but showed a wider range of surface ornamentation of the tegillum, varying from

shagreenate to granulate, and exhibiting occasional development of trabeculae joining the process tips.

Intraspecific morphotypes. None.

Comparison. *Spiniferites ramosus sensu lato* of Rochon et al. (1999) differs from *Spiniferites bulloideus sensu Wall (1965)* primarily in its uniform, slender processes, the latter having two membranous, stout antapical processes.

Remarks. *Spiniferites ramosus*, the type of *Spiniferites*, was first described by Ehrenberg (1837, as *Xanthidium ramosum*) from the Upper Cretaceous (Senonian) of Germany. Ehrenberg did not designate a holotype and provided drawings without a description. Davey & Williams (1966, p. 33–34) emended the description of *Spiniferites* and designated Ehrenberg's *Xanthidium ramosum* as the type. *Spiniferites ramosus* was redescribed by Davey & Williams (1966) as being thin-walled with a smooth, reticulate or granular wall, with gonol and intergonol processes. They described seven varieties of this species, with the typical variety, *Spiniferites ramosus* var. *ramosus*, described as bearing gonol and occasional intergonol processes, which are sometimes branched. There was no description of the wall structure of the type variety. The size ranges reported by Davey & Williams (1966) for *Spiniferites ramosus* var. *ramosus* were 34–41 µm, with process lengths 5–13 µm. During the first workshop it became clear that most researchers use the description and illustrations of Rochon et al. (1999, p. 38, pl. 9, figs. 4–6) as a conceptual benchmark for *Spiniferites ramosus*. In this sense, *Spiniferites ramosus* has a smooth wall, exclusively gonol, long processes with low sutural crests and no apical boss; the reported central body length reported by Rochon et al. (1999) is 30–46 µm. LL suggested that this concept corresponds to *Spiniferites ramosus* subsp. *ramosus*; KNM said that the description of *Spiniferites ramosus* subsp. *ramosus* is much broader and therefore it would be less ambiguous to use "*Spiniferites ramosus sensu Rochon et al. 1999*", as done here, to refer to this particular morphology encountered in the Quaternary. This form is further discussed by Gurdebeke et al. (2018).

KNM considered that *Spiniferites ramosus* var. *ramosus sensu Davey & Rogers 1975* cannot be attributed to *Spiniferites ramosus sensu Rochon et al. (1999)* but should rather be attributed to *Spiniferites belerius* or *Spiniferites bulloideus sensu Wall 1965*.

MJH noted in draft that specimens described and illustrated by Rochon et al. (1999) were in fact referred to *Spiniferites ramosus sensu lato*, and calling them "*Spiniferites ramosus sensu Rochon et al. 1999*" does not fully capture the intent of these authors, although understandably "*Spiniferites ramosus sensu lato sensu Rochon et al. 1999*" is an impractical label. In the longer term, a solution using formal nomenclature would be preferable.

2.31. *Spiniferites ramosus subsp. multiplicatus (Rossignol 1964) Lentin & Williams 1973*

Synonymy. *Hystriosphera furcata* var. *multiplicata* Rossignol 1964, pl. 1, fig. 14; pl. 3, fig. 16.

"*Hystrichosphaera ramosa* var. *multiplicata*" Harland & Downie, 1969, fig. 5 [combination not validly published]. non *Spiniferites hyperacanthus* (Deflandre & Cookson) Sarjeant 1970 [Matsuoka (1985a, p. 35) proposed the synonymy of *Spiniferites ramosus* subsp. *multiplicatus* with *Spiniferites hyperacanthus* (Deflandre & Cookson) Sarjeant 1970, but we follow de Vernal et al. (1992, p. 325) and Londeix et al. (2009, p. 66) in not accepting this synonymy.]

Holotype. Rossignol 1964, pl. 1, fig. 14; de Vernal et al. 1992, pl. 8, fig. 9.

Type locality. Ashdod borehole, coastal plain, Israel.

Type stratum. Pleistocene or Holocene (Rossignol 1964).

Etymology. Although not mentioned by Rossignol (1964), from Latin *multiplicus* (composed of many elements), presumably in reference to the presence of intergonal processes.

Distinguishing characters. Central body is ovoid, bearing one or two intergonal processes that are bifurcated and present on every suture. The wall is thick – comparable in thickness to *Spiniferites pachydermus* – with a smooth to granular wall surface. The shape, size and tabulation of the cyst are similar to those of *Hystrichosphaera furcata* (now considered a synonym of *Spiniferites ramosus*). The two main dorsal antapical processes are pronounced. (Based on Rossignol 1964, p. 86.)

Dimensions: Central body 44 x 40 µm, process length 15–20 µm (Rossignol 1964).

Biological affinity. Unknown.

Intraspecific morphotypes. None.

Comparison. The presence of one or two occasional intergonal processes distinguishes this subspecies from *Spiniferites ramosus* subsp. *ramosus* and from *Spiniferites bulloideus*. It differs from *Spiniferites hyperacanthus* by having only occasional intergonal processes, by its more ovoid shape and the common occurrence of septa.

Remarks. This taxon has been recorded only by Harland & Downie (1969, pl. 7, fig. 5), Bradford & Wall (1984, pl. 4, figs. 15–17; pl. 5, figs. 1–3, 5–7), and Londeix et al. (2009, p. 66, not depicted). During the second workshop, KNM wondered if the specimens that he identified as *Spiniferites ludhamensis* from topotype material from the Ashdod borehole were what Rossignol (1964) had described and depicted as *Hystrichosphaera furcata* var. *multiplicata*. KNM noted in draft that Rossignol (1964, p. 86) specified that "This variety may have a wall thickness similar to the variety *pachyderma*"; however, all other details of the wall structure are lacking. LL explained in draft that he considers *Spiniferites ramosus* subsp. *multiplicatus* to accord with the concept illustrated by the holotype drawing of *Spiniferites ramosus* subsp. *multiplicatus* – that is to say similar to *Spiniferites ramosus* var. *ramosus* but with consistent intergonal processes. For him, the consistent presence of intergonal processes is the most important characteristic for *Spiniferites ramosus* subsp. *multiplicatus*, as it was the first characteristic noted by Rossignol in her original description of this taxon and is featured in the name. LL mentioned that the thick and granular wall that this subspecies "may have" is uncommon, and

allows for variation in wall structure between smooth and granular.

2.32. *Spiniferites rhizophorus* Head in Head & Westphal 1999 (Plate 6, figures 1–15)

Synonymy. None.

Holotype. Head & Westphal 1999, fig. 6, nos. 1–4.

Type locality. Clino Borehole, Great Bahama Bank, Caribbean Sea.

Type stratum. Upper Lower Pliocene (Head & Westphal 1999).

Etymology. Named in reference to the stilt-like branching of process bases, which recalls the aerial roots of the mangrove *Rhizophora* (Head & Westphal 1999).

Distinguishing characters. The central body wall appears unstratified under light microscopy and has a nearly smooth (finely and faintly granulate/punctate) tegillum. The central body is broadly ovoid with a very small apical protuberance. The processes are gonial, trifurcate (usually with secondary bifurcations) and solid, with some branched and stilt-like bases, reminiscent of the aerial roots of the mangrove tree *Rhizophora*. The sutures are reflected by faint lines or low solid ridges. The apex is indicated by a tapering, spine-like, hollow process with smaller side branches. The archeopyle is formed by loss of plate 3", slightly reduced. (Based on Head & Westphal 1999, p. 15–17.)

Dimensions. Central body length 38 (46.0) 51 µm; average process length 9 (14.0) 17 µm (Head & Westphal 1999).

Biological affinity. Unknown.

Intraspecific morphotypes. None.

Comparison. During the first workshop, MJH remarked that the drawings of the processes of *Spiniferites? tripodes* in Morzadec-Kerfourn (1966, as *Baltisphaeridium tripodes*) are similar to the stilt-like columns of the processes of *Spiniferites rhizophorus*, and he suggested that the holotype or topotype material of the former species should be examined for comparison with *Spiniferites rhizophorus*. Presently, the unclear original description and illustration of *Spiniferites? tripodes* does not permit a detailed comparison.

Remarks. None.

2.33. *Spiniferites ristingensis* Head 2007 (Plate 7, figures 1–15)

Synonymy. *Spiniferites* sp. 1. Head et al. 2005, figs. 9d–g.

Holotype. Head 2007, figs. 8c–l.

Type locality. Ristinge Klint, Denmark.

Type stratum. Eemian sediments of the Baltic Sea (Head 2007).

Etymology. Named after the type locality (Head 2007).

Distinguishing characters. This species has an ovoid central body, with or without a short apical protuberance, and bears membranous gonial processes joined by low sutural crests. Some processes are distally expanded to form irregular polygonal platforms. The central body wall is formed of two wall layers of similar thickness. The pedium is smooth, and the tegillum forms small, densely distributed blisters and

hollow undulations over the surface (loosely comparable to bubble-wrap). The processes and sutural crests are formed by the tegillum and are distinctly bilayered. The surface of the processes and sutural crests appears granulate. (Based on Head 2007, p. 1011–1012.)

Dimensions. Central body length 39 (43.0) 49 μm ; wall thickness 1.0–1.8 μm ; maximum process length 11 (12.9) 17 μm (Head 2007).

Biological affinity. Unknown.

Intraspecific morphotypes. None known.

Comparison. *Spiniferites ristingensis* is distinguished by its membranous processes and the distinctive wall structure of the central body. *Spiniferites ludhamensis*, from the Upper Pliocene of eastern England, has a similar wall structure but has hollow, non-membranous processes and hollow sutural crests. *Spiniferites delicatus* from modern sediments off the British Isles has processes of similar shape but connected by high sutural crests, and a central-body wall structure characterised by a pedium with radial fibers and a thin granular tegillum whose surface appears microgranular to microreticulate. *Spiniferites delicatus* also differs in having a reduced archeopyle. (Based on Head 2007.) For *Spiniferites alaskensis*, see section 2.6.

Remarks. During the first workshop, VP wondered whether the wall structure of *Spiniferites ristingensis* is comparable to the wall structure of *Hafniasphaera*. MJH and LL did not think this is comparable to *Hafniasphaera* because the wall structure of *Spiniferites ristingensis* is not firmly vacuolate as in *Hafniasphaera*. During the second workshop there was also doubt as to whether the difference between *Spiniferites ristingensis* and *Spiniferites delicatus* warrants two separate species. KNM mentioned during draft that he has seen this species in recent sediments in the Gulf of Cádiz, offshore Portugal, the Baltic and Black seas, and Baie de la Vilaine (Brittany). SR added during drafting that *Spiniferites ristingensis* is abundant (up to about 10% of the cyst assemblages) in modern sediments off southwestern Portugal, where it occurs with *Spiniferites delicatus*.

2.34. *Spiniferites scabratus* (Wall 1967) Sarjeant 1970 (Plate 8, figures 1–6)

Synonymy. *Hystriosphera scabrata* Wall 1967, p. 102, pl. 14, figs. 10–13; text-fig. 2.

Holotype. Wall 1967, pl. 14, figs. 10–13; Harland 1983, pl. 45, fig. 7.

Type locality. Core A254/330, Yucatan Basin, 19° 35' N. 84° 51' W; Caribbean Sea.

Type stratum. Holocene; depth 150 cm (Wall 1967).

Etymology. Although not mentioned by Wall (1967), the epithet presumably refers to a scabrate tegillum.

Distinguishing characters. The central body is ovoid with a circular displacement of one cingulum width. The septa are microgranular and undulating. The processes are exclusively gonial; there is a complex process at the anterior end of the sulcus. There are three to four apical plates. The archeopyle is rounded. The sulcus is straight with the sulcal plates sometimes visible, particularly the posterior sulcal plate. (Based on Wall 1967, p. 102.)

Dimensions. Central body length 48–55 μm ; process length 10–17 μm (Wall 1967).

Biological affinity. The cyst–theca relationship was described, but not illustrated, by Wall & Dale (1968, p. 271) as follows: “A resting spore identified as *Hystriosphera scabrata* Wall (using fossil terminology) from the Gulf of Paria was incubated to give a motile *Gonyaulax* theca of the *spinifera* type (48 x 38 μm) without antapical spines and with very indistinct ornamentation. The theca was very delicate and could not be identified with any species.”

Intraspecific morphotypes. A similar cyst was depicted by Matsuoka (2005) as *Spiniferites* sp. cf. *scabratus* in Holocene sediments off Santa Cruz Island (Galapagos). The difference between Matsuoka’s form and *Spiniferites scabratus* is not clear.

Comparison. Wall (1967) remarked that the difference between *Spiniferites scabratus* and *Spiniferites membranaceus* is the presence of a strong antapical flange in the latter.

Remarks. MJH noted that it is not clear whether one or two specimens were assigned as holotype, and thus questioned the validity of the name. However, personal communication with David Wall confirmed that it is a single specimen that was rotated into different views. KZ remarked that the wall is nearly smooth, and it is hard to see scabrate septa. PJM stated that the holotype looks oxidised, and the slide is in poor shape. KNM said that the processes are relatively broad and short and also noted that this species was recorded from Trondheimsfjord, Norway, by Dale (1976, pl. 1, fig. 6). However, at the second workshop a specimen considered to be *Spiniferites scabratus* by BD was identified as *Spiniferites ristingensis* by MJH and KNM. MJH in draft provided the following observations of the holotype: The central body is ovoidal, with no apical protuberance. The wall surface appears strongly granulate in plan view, although upon closer inspection the granules seem to be discrete solid rods forming a columellate layer that separates two thin wall layers. The rods are $\sim 0.6 \mu\text{m}$ or less in diameter and are separated from one another by their own width. The entire wall thickness is $\sim 1.0 \mu\text{m}$. Processes have a scabrate surface, are hollow and wide at their base, and terminate in slender trifurcations that project at right angles. Only gonial processes were seen. Adjoining sutural crests are hollow. The archeopyle is not reduced, its margin closely following the sutures.

2.35. *Spiniferites septentrionalis* Harland 1977 (Plate 8, figures 7–9)

Synonymy. *Spiniferites aquilonius* Matsuoka & Bujak 1988, p. 74–76, pl. 11, figs. 6a–d; pl. 12, figs. 1a–b; pl. 19, figs. 4a–c, 7; text-figs. 17A–E. [fide Matsuoka in Head & Wrenn (1992, p. 26)]. non *Achomosphaera andalusiensis* Jan du Chêne 1977. non *Spiniferites ramuliferus* (Deflandre 1937) Reid 1974.

Holotype. Harland 1977, pl. 1, figs. 17–18.

Type locality. Borehole SLN 75/33, north-central North Sea.

Type stratum. Upper Quaternary (Harland 1977).

Etymology. From the Latin *septentrionalis* (northern, northerly), in reference to the occurrence of the type material in North Sea sediments (Harland 1977).

Distinguishing characters. Central body ovoid to spheroidal with a shagreenate to scabrate or papillate outer wall, with or without a small apical boss. Generally no tabulation is visible except for the archeopyle. Processes are long, slender, and gonol only. The shafts of the more membranous processes are commonly moderately perforate. The processes vary distally from being trifurcate with bifid tips to being trifurcate with perforate or fenestrate distal ends: the latter structure is especially prominent on the cingular processes. The archeopyle is simple, reduced, and formed by the loss of plate 3". (Based on Harland 1977, p. 103–104, and new observations of the holotype made by LL and KNM.)

Dimensions. Central body length 33.75 (40.52) 47.50 μm , width 27.50 (31.04) 37.50 μm ; wall thickness 1.0–2.0 μm ; process length 10.00 (12.40) 16.25 μm (Harland 1977).

Biological affinity. Unknown.

Intraspecific morphotypes. None.

Comparison. Although *Achomosphaera andalousiensis* was considered a synonym of *Spiniferites septentrionalis* by Harland (1983, p. 326) and Jan du Chêne & Londeix (1988, p. 421), the synonymy was questioned by Head & Wrenn (1992, p. 2). During the first workshop, participants expressed a general difficulty in understanding the difference between *Achomosphaera andalousiensis* and *Spiniferites septentrionalis*, and wondered if they could be synonymous. During the first workshop, LL considered specimens illustrated by SEM in Harland (1988, pl. 81, as *Achomosphaera andalousiensis*) to belong to a species other than *Achomosphaera andalousiensis* (particularly specimen MPK 5925). LL and MJH expressed the need to examine the holotype of *Spiniferites septentrionalis* to determine whether or not it is conspecific with *Achomosphaera andalousiensis*. In draft, James B. Riding subsequently provided numerous photographs of the holotype. Through study of these new images, LL and KNM confirmed *Spiniferites septentrionalis* can be separated from *Achomosphaera andalousiensis* on the basis of having a more elongate central body, a shagreenate to scabrate or papillate wall (sensu Williams et al. 2000), and distal terminations of the processes that are fenestrate (rather than trabeculate); the fenestrations may not be on all trifurcations, a contrast to the more regular process morphology in *Achomosphaera andalousiensis*. However, MJH remarked in draft that the difference between the two species is not so straightforward, and that a SEM micrograph of a specimen of *Achomosphaera andalousiensis* in Harland 1988 (Plate 81, Figure 4) shows a transition to the genus *Spiniferites*. LL moreover suggested in draft that "if you look attentively at the central body surface of *Spiniferites septentrionalis*, there are faint ridges and almost always septa around plate 3". In addition to the differences in process terminations, *Achomosphaera andalousiensis* sometimes exhibits faint ridges, but no septa (see SEM micrographs in Jan du Chêne 1977, Jan du Chêne & Londeix 1988, Warny 1999). To keep *Spiniferites septentrionalis* in the genus *Spiniferites* is a way to retain this difference. That is why I do not support transferring *Spiniferites septentrionalis* to *Achomosphaera*." Therefore, the synonymy between *Achomosphaera andalousiensis* and *Spiniferites septentrionalis* is not followed here. See further discussion in Londeix et al. (2018). The perforate process bases are

similar to *Spiniferites lazus* but the latter does not possess fenestrate distal ends (Harland 1977, p. 103).

Remarks. Harland (1977, p. 103) mentioned that Reid (pers. comm. to Harland) is of the opinion that *Spiniferites ramuliferus*, as recorded by him (1974), is synonymous with *Spiniferites septentrionalis*, but we consider Reid's specimen to belong to *Achomosphaera ramosasimilis*.

2.36. *Spiniferites spinatus* (Song Zhichen in Song Zhichen et al. 1985) Lentin and Williams 1989

Synonymy. *Spiniferites cingulatus* (Wetzel 1933) Sarjeant 1970 var. *spinatus* Song Zhichen in Song Zhichen et al. 1985, p. 43, pl. 2, fig. 5.

Holotype. Song Zhichen in Song Zhichen et al. 1985, pl. 2, fig. 5.

Type locality. ~300 km east of Hangzhou Bay, East China Sea.

Type stratum. Lower Quaternary (Song Zhichen et al. 1985).

Etymology. Not provided by Song Zhichen in Song Zhichen et al. (1985), but probably from the Latin *spinatus* for spine-bearing, in reference to the occurrence of processes.

Distinguishing characters. Central body ovoid to subspheroidal, the epicyst and hypocyst being equal in size and separated by a wide and pronounced cingulum. The cyst wall probably consists of two layers, and is relatively thin with a coarse to granular surface. Sutures form smooth ridges 2–3 μm high. At junctions there are short tubular processes, which are narrow and hollow with trifurcate or bifurcate distal ends. Between each pair of gonol processes are at least two intergonol processes each with a wide base that abruptly tapers to a pointed end distally. Tabulation is typical for the genus, but the archeopyle is not clear. (Based on Song Zhichen in Song Zhichen et al. 1985, p. 43, translation by HG.)

Dimensions. Central body diameter 38 μm ; process length 5 μm (Song Zhichen in Song Zhichen et al. 1985).

Biological affinity. Unknown.

Intraspecific morphotypes. None.

Comparison. None.

Remarks. This taxon was initially described as a process-bearing variety of *Spiniferites? cingulatus* (Wetzel 1933) Sarjeant 1970 (now *Pterodinium cingulatum* (Wetzel 1933) Below 1981) from the Senonian (Cretaceous), a species that is probably not closely related. It is difficult to assess whether *Spiniferites spinatus* is conspecific with *Spiniferites hyperacanthus* given the lack of a detailed description and an unclear image. We therefore suggested that the name *Spiniferites spinatus* be restricted to the holotype.

2.37. *Spiniferites strictus* Matsuoka 1983 (Plate 8, figures 10–12)

Synonymy. None.

Holotype. Matsuoka 1983, pl. 12, figs. 5a–b.

Type locality. Takani-shinden, Nishiyama-cho, Niigata Prefecture, central Japan.

Type stratum. Nishiyama Formation; Pliocene or younger (Matsuoka 1983).

Etymology. From the Latin *strictus* (drawn tight), in reference to the stout processes.

Distinguishing characters. The central body is subspheroidal to ovoid with a smooth to granular outer wall: some specimens have a small apical boss. The processes are both gonial and intergonial, and the process bases are sometimes perforated. (Based on Matsuoka 1983, p. 136–137.)

Dimensions. Central body length 53–67 µm, width 50–62 µm; process length 10–14 µm; holotype wall thickness 2 µm (Matsuoka 1983).

Biological affinity. Unknown.

Intraspecific morphotypes. None.

Comparison. Matsuoka (1983) stated that *Spiniferites strictus* is similar to *Spiniferites bentorii*, but differs by having many short intergonial processes.

Remarks. VP remarked during the first workshop that *Spiniferites strictus* is similar to *Spiniferites bentorii*, but noted that she had not seen the material. However, LL did not agree that the two species look similar. This species is discussed by Limoges et al. (2018).

2.38. *Spiniferites? tripodes* (Morzadec-Kerfourn 1966) Lentin & Williams 1973

Synonymy. *Baltisphaeridium tripodes* Morzadec-Kerfourn 1966, p. 140–141, pl. 3, figs. 3–4.

Holotype. Morzadec-Kerfourn 1966, pl. 3, figs. 3–4.

Type locality. Borehole 36, drilled in 1961–1962, Marais de la Vilaine, south of Redon, France.

Type stratum. Holocene (Morzadec-Kerfourn 1966).

Etymology. From the Latin *tri* (three) and *podes* (feet) (Morzadec-Kerfourn 1966).

Distinguishing characters. The central body is spheroidal and smooth walled. The base and top of each appendage are separate, and some fenestrations may occur at mid-length. Based on Morzadec-Kerfourn (1966, p. 140–141).

Dimensions. Central body diameter 45 µm; average process length 18 µm (Morzadec-Kerfourn 1966).

Biological affinity. Unknown.

Morphotypes. None.

Comparison. See *Spiniferites restingensis*.

Remarks. *Spiniferites? tripodes* was also recorded by Morzadec-Kerfourn (1979, from the Pelagian Sea, east of Tunisia) and by Morzadec-Kerfourn (1984, from the Rhone Delta, as *Spiniferites* cf. *tripodes*). During the first workshop, there was general agreement that this species is not well understood. LL noted that it has been illustrated three times by Morzadec-Kerfourn, and each time it looked different. We suggest that for now *Spiniferites? tripodes* be restricted to the holotype.

3. Species previously assigned to *Spiniferites* but here considered or accepted as belonging to other genera

3.1. *Impagidinium inaequalis* (Wall & Dale in Wall et al. 1973) Londeix et al. 2009 (Plate 9, figures 1–6)

Synonymy. *Spiniferites inaequalis* Wall & Dale in Wall et al. 1973, p. 22, pl. 1, figs. 7–8.

Holotype. Wall et al. 1973, pl. 1, figs. 7–8.

Type locality. Core 1474P, southeastern Black Sea.

Type stratum. Lower Holocene; 725 cm (Wall et al. 1973).

Etymology. Presumably in reference to the uneven shape of the broad hypocyst compared with the flask-like (lageniform) epicyst.

Distinguishing characters. Cysts with a lageniform (flask-like) shape and an unevenly broad hypocyst. The lageniform epicyst is subcylindrical to campanulate with weakly tapering lateral surfaces; it has a smoothly rounded apex with an apical boss and expanded posterior precingular surfaces. The cingulum is situated at the cyst's mid-length and is in the form of a descending spiral, the ends displaced by one cingulum width. The “lopsided” hypocyst is broader than the epicyst and is irregularly subrectangular with a broad, flat antapex, the width of which equals that of the cyst near the cingulum. The sulcus is almost vertical and narrow, and equivalent in width to approximately one fifth of the width of the hypocyst except at the antapex, where it expands. In lateral view the cyst is irregularly subrectangular. A perfect tabulation is reflected by low sutural ridges. Several features of the tabulation are of special interest. On the epicyst, the mid-ventral anterior sulcal plate is extensive and contacts both 5' and 6'. On the hypocyst, plate 1p is large and subrectangular, while the antapical plate 1''' and the sulcal plates are transversely elongated. Very small gonial spines occur on some specimens, sometimes barely visible. The archeopyle is formed by loss of plate 3". The wall is scabrate to microgranular. (Based on Wall et al. 1973, p. 22.)

Dimensions. Central body length (without processes) 44–55 µm, width 33–43 µm; processes up to 5 µm long (Wall et al. 1973).

Biological affinity. Unknown.

Intraspecific morphotypes. None.

Comparison. The peculiar shape of the central body makes this species unique.

Remarks. The species was also found in recent sediments from the Black Sea and Marmara Sea by Mudie et al. (2002). During the first workshop, LL explained that he had reattributed *Spiniferites inaequalis* to *Impagidinium* because occasional “very small gonial spines” or “minute projections” is not enough to assign the species to the genus *Spiniferites*. *Spiniferites cingulatus* and *Spiniferites crassimuratus* (Davey & Williams 1966) Sarjeant 1970 were transferred for similar reasons to *Pterodinium* by Below (1981) and Thurow et al. (1988), respectively. Although not specified by Londeix et al. (2009), the species also accords with *Impagidinium* because plate 6' is triangular and contacts 4' (Wall et al. 1973, pl. 1, fig. 8). PJM noted that she has observed well-preserved specimens of this species in mid-Pleistocene to Holocene sediments of the northern Caspian Sea (Volga and Emba deltas), as well as in Upper Miocene material from the Black Sea provided by FS. BD stated in draft that “very small spines or minute projections are accepted for maintaining species as ecophenotypes within the genera *Operculodinium*, *Lingulodinium*, and *Spiniferites* from low salinity environments such as the Black Sea and the Baltic (Dale 1996), and therefore he accepts *Spiniferites inaequalis* within *Spiniferites*. MJH

added in draft his following observations of the holotype: Its central body has a slight apical protuberance about 1.5 µm high, a fairly thick (~0.8–1.0 µm) wall, and an irregularly granulo-reticulate surface, with muri/granules about 0.3 µm or less in width. The sutural crests reach ~2.0 µm high, and are solid except at the base (minutely suturocavate). Processes are gonol, up to ~1.0 µm in length, solid, unbranched, and taper to blunt points. The cingulum displaced by about 1 width. The archeopyle margin follows the sutures quite closely. MJH further remarked that it may be premature to transfer this species to the genus *Impagidinium*. The processes, while small for a species of *Spiniferites*, are discrete elements rather than extensions of the crests as found for example in *I. aculeatum*. Given the extreme morphological plasticity of many Paratethyan forms, MJH wonders how *Spiniferites inaequalis* compares with the full range of morphology exhibited by *Spiniferites cruciformis*, which is found in the same samples. He presently accepts the name *Spiniferites inaequalis*.

3.2. *Spiniferites? rubinus* (Rossignol 1962 ex Rossignol 1964) Sarjeant 1970

Synonymy. “*Hystrichosphaeridium rubina*” Rossignol 1962, p. 134 [invalid because no illustration provided].

Hystrichosphaera rubina Rossignol 1962, p. 134 ex Rossignol 1964, p. 87–88, pl. 1, figs. 12–13, pl. 3, figs. 22–23.

Holotype. Rossignol 1964, pl. 1, figs. 12–13.

Type locality. Borehole close to Rubin 23/0, coastal plain, Israel.

Type stratum. Quaternary; depth 160–166 m (Rossignol 1964).

Etymology. Named after a stream called Wadi Rubin (Rossignol 1964).

Distinguishing characters. An ovoid cyst with a micropunctate or faintly and finely granular wall that also makes up the processes and sutural membranes. The tabulation is unclear, but plate areas 4' and 1' can be recognised. The cingulum and sulcus are also usually conspicuous, but do not exhibit individual plates. The sulcus is broad and the cingulum is a laevorotatory helicoid, planar to displaced by one-half of its width, and not indented. Processes are gonol and membranous and are most conspicuous in the apical, antapical, cingular, and sulcal areas. They are somewhat flexuous and have petaloid tips. Some specimens have many membranes especially in the areas listed. The sulcus is so broad and is often surrounded by such high membranes that the cyst appears to bear membranes only around its margin. However, membranes may not be developed between the sulcus and the adjacent pre- and postcingular regions. In these forms some of the non-membranous processes appear as small protuberances. Complex boxlike processes also occur at the apex of the sulcus and in the position of the posterior intercalary plate. Some of the more complex membranous processes carry small spines. In specimens that exhibit more obvious processes, those in the cingular region are erect, simple, slender, and conical. The archeopyle is

formed by the loss of plate 3". (Based on Rossignol 1964, p. 134, Harland 1979, p. 537, and Head 1996b, p. 560.)

Dimensions. Central body length 52 µm, height 44 µm; crest height 15–20 µm (Rossignol 1964). Central body length 46 (53.0) 61 µm, equatorial diameter 47 (49.5) 53 µm; maximum crest height 10–11 µm (Head 1996b). Central body length excluding processes or membranes 46.0–54.0 µm, width 38.0–46.0 µm; maximum process length or membrane height 10.0–12.0 µm (Harland 1979).

Biological affinity. Unknown.

Intraspecific morphotypes. None.

Comparison. None.

Remarks. During the first workshop, KNM questioned whether this species really is a *Spiniferites*. MJH remarked that it is like a *Spiniferites*, but also resembles *Invertocysta lacrymosa* Edwards 1984. LL asked “why not *Pentadinium* Gerlach 1961?” MJH replied that when the tegillum retracts, you get the resemblance of a continuous spine-like structure; see for instance specimens illustrated by Harland (1979, pl. 2, fig. 4–11), which represent one end of the spectrum. LL considered that it does not belong in *Spiniferites*, but was uncertain where else it could go. Since there are no processes on this species, it cannot remain in *Spiniferites*. It is approaching *Impagidinium* (if the septa are solid) or *Pentadinium* (if the septa form sutural pericoels), but could also be questionably assigned to *Invertocysta*. MJH agreed. PJM remarked after the first workshop that “the specimens of *Spiniferites rubinus* I have seen in the North Atlantic are clearly different from *Invertocysta* in periphragmal attachment, size and arrangement. I have seen no signs of intermediates.” There was consensus that this species does not belong to *Spiniferites*, but that no existing genus could be identified that would accommodate it; so for now the species is retained questionably in *Spiniferites*.

3.3. *Thalassiphora balcanica* Balteş 1971

Synonymy. *Disphaeria balcanica* (Balteş 1971, p. 6, pl. 3, figs. 3–7) Norvick 1976, p. 99.

“*Subathua balcanica*” (Balteş 1971, p. 6, pl. 3, figs. 3–7) Khanna & Singh 1980, p. 308 and 1981b, p. 394. [Combination not validly published].

Spiniferites balcanicus (Balteş 1971, pl. 3, figs. 3–7) Sütő-Szentai 2000, p. 162.

Holotype. Balteş 1971, pl. 3, figs. 3–7.

Type locality. Pannonian Basin, Romania.

Type stratum. Lower Pliocene, Pontian regional stage (Balteş 1971).

Etymology. Presumably in reference to the Balkan Peninsula, which includes Romania.

Distinguishing characters. The description of Balteş (1971, p. 6) indicates that the holotype of *Thalassiphora balcanica* from Romania is a very large (120–130 µm) cyst with an ellipsoid central body partly enfolded in a membranous outer wall that contacts the central body only on one side (dorsal side? [sic]). Balteş described the wall surface as pterate and fibrous, quasi-reticulate and perforate, resembling a lamellate wing. Balteş described the central body as having a

vaguely outlined cingulum, and a trapezoidal cingular archeopyle, but otherwise lacking tabulation. However, Sütő-Szentai (2000, p. 162) transferred *Thalassiphora balcanica* to *Spiniferites* as *S. balcanicus*, based on specimens from Upper Pannonian deposits in boreholes from Hungary, some of which are illustrated as having highly reduced, undecipherable ornamentation and others with fenestrate luxuria and attachments like those of *Galeacysta etrusca* (see Mudie et al. 2018). The emended diagnosis of Sütő-Szentai (2000) for *Spiniferites balcanicus* describes an ovoid or spheroidal central body with two membranes “fixed both on the right and left side of the sulcus” and sometimes with two wing-like membranes that are “differently perforated”, one of them being arched in the apical area and being partially connected except in the ventral area.

Dimensions. Central body length 90–100 µm, total length 120–130 µm; archeopyle 35–45 µm (Balteş 1971). Central body length 80–90 µm, total length 80–110 µm (Sütő-Szentai 2000).

Biological affinity. Unknown.

Intraspecific morphotypes. None.

Comparison. At the second workshop, PJM suggested that this taxon may be the same as the Late Eocene informal species “*Thalassiphora subreticulata*” of Fensome & Williams (2005). The camocavate species described by Balteş clearly differs from *Galeacysta etrusca*, which has a completely different non-fibrous tegillum and has a galeate (helmet-shaped) tegillum with tabulate claustra (i.e., very large, arch-shaped/camerate fenestrations), and with a completely different attachment to the endocyst than the membranous, enveloping, perforate tegillum of *Thalassiphora balcanica*. In addition, the light microscope images of three specimens of *Spiniferites balcanicus* from the Paks 4 borehole (Sütő-Szentai 2000, pl. IX, figs. 1–3) neither demonstrate the features Maria Sütő-Szentai describes nor do they support her differential diagnosis in which she distinguishes *Spiniferites balcanicus* from *Subathua balcanica*.

Remarks. *Subathua balcanica* is invalidly published because the basionym was not fully referenced; Stover & Evitt (1978, p. 194) considered *Thalassiphora pelagica* to be the senior synonym of this taxon.

During the first workshop there was a general discussion as to why *Thalassiphora balcanica* might belong to *Spiniferites*, as suggested by Sütő-Szentai (2000). PJM added in draft that this assignment was based on the comments in the paper by Sütő-Szentai (2000) that mention gonyaulacoid tabulation marked by “stumps of processes” in some but not all cysts which “... probably depends on stage of ontogeny”. However, these processes have not been observed in samples examined during the workshops and the cysts PJM has seen show many characteristics of *Thalassiphora*. Given these observations, it seems prudent to assume that the species indeed belongs to *Thalassiphora*, since it had been originally described as *Thalassiphora baltica*. The suggestion was also expressed that the species could belong to *Hystriochostrogylon*. There was general agreement that this is not a *Spiniferites* species and therefore we retain it in *Thalassiphora*.

Mudie et al. (2018) found no intergradation in morphology between *Thalassiphora balcanica* and *Galeacysta etrusca* other than possibly some overlap at the upper end of their endocyst-ectocyst size and these authors agree to retain *Thalassiphora balcanica*. PJM stated that the location of the holotype (Balteş’s specimen L/C. 6229 -44/106) is now unknown and the lectotype designated by Sütő-Szentai (2000) as *Spiniferites balcanicus* held by Maria Sütő-Szentai at Komló, in southwestern Hungary, are severely dessicated, requiring new studies of material from the type locality. Detailed morphological studies of specimens from northern Croatia are currently under investigation by PJM, AR, Rob Fensome and Koraljke Bakrač (Croatian Geological Survey).

4. Discussion about genus/species/variety concepts

During the round table discussion held at the second workshop, several themes were discussed, the major foci being: 1) what to do with problematic species; 2) concepts in/of *Spiniferites* taxonomy (what constitutes a genus, species, variety and forma); and 3) dual versus unified taxonomy (see also Ellegaard et al. 2018). This discussion can be found in [Supplementary Appendix 3](#).

Acknowledgements

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